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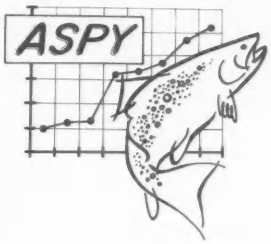

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Foreword

The Information and Publications Branch has a proud tradition of publishing benchmark symposium proceedings which have become internationally celebrated classics in aquatic biology and ecology. It has been privileged to publish four sponsored by the Great Lakes Fishery Commission over the past 15 years.

These proceedings are particularly noteworthy in documenting man's impact on the Great Lakes and the severity of various environmental perturbations, especially degradation of habitat through urban development and pollution. They include the international symposium on Salmonid Communities in Oligotrophic Lakes (SCOL) (J. Fish. Res. Board Can. 29, No. 6), 1972; the Percid International Symposium (PERCIS) (J. Fish. Res. Board Can. 34, No. 10), 1978; the Sea Lamprey International Symposium (SLIS) (Can. J. Fish. Aquat. Sci. 37, No. 11), 1979; and the Stock Concept Symposium (STOCS) (Can. J. Fish. Aquat. Sci. 38, No. 12), 1980. With this issue we publish the fifth: the International Symposium on Assessment of Stocks and Prediction of Yield (ASPY) (Can. J. Fish. Aquat. Sci. 44, Suppl. 2), 1987.

In contrast with SCOL which documented degradation, ASPY documents the rehabilitation process. Its purpose was to estimate total fish production potential of the Great Lakes and determine the proportion of that production necessary for continuing maintenance and rehabilitation of the fish-producing system.

Taking advantage of relaxed surroundings in Quetico Centre in northern Ontario, symposium participants immersed themselves for 2 weeks in issues relating to community metabolism and its allocation to maintenance, rehabilitation, and harvest. During week 1, they presented case histories, and recent developments and new analytical models in terrestrial and theoretical ecology with possible application to rehabilitation of fish communities in the Great Lakes. Week 2 was devoted to marshalling this background information, weaving into it the major trends or broad generalizations emerging during the previous week, and producing synthesis papers. It is these background and synthesis papers which comprise the ASPY presentation.

The *Journal* salutes the symposium's sponsors and participants, and is proud to present their findings and conclusions for application to Great Lakes fishery management. This *Journal* Supplement is a tribute to all those who have played a role in its organization, production, and dissemination.

JOHANNA M. REINHART
Director and Editor

Préface

La Direction de l'information et des publications a toujours été fière de publier les comptes rendus de colloques faisant autorité, qui sont devenus des ouvrages classiques de réputation internationale dans les domaines de la biologie et de l'écologie aquatiques. Elles a eu le privilège, au cours des 15 dernières années, de publier le compte rendu de quatre colloques parrainés par la Commission des pêcheries des Grands Lacs.

Ces comptes rendus sont particulièrement remarquables du fait qu'ils exposent les effets des activités humaines sur les Grands Lacs et la gravité des diverses perturbations environnementales, en particulier la dégradation de l'habitat entraînée par l'urbanisation et la pollution. Il s'agit des comptes rendus des colloques suivants : Salmonid Communities in Oligotrophic Lakes (SCOL) (J. Fish. Res. Board Can. 29, n° 6), 1972; Percid International Symposium (PERCIS) (J. Fish. Res. Board Can. 34, n° 10), 1978; Sea Lamprey International Symposium (SLIS) (Can. J. Fish. Aquat. Sci. 37, n° 11), 1979; et Stock Concept Symposium (STOCS) (Can. J. Fish. Aquat. Sci. 38, n° 12), 1980. À ceux-ci vient maintenant s'ajouter le compte rendu du colloque international Assessment of Stocks and Prediction of Yield (ASPY) (Can. J. Fish. Aquat. Sci. 44, Suppl. 2), 1987.

Contrairement au colloque SCOL qui portait sur la dégradation de l'habitat, le colloque ASPY concerne le processus de rétablissement. Il visait l'estimation du potentiel de production totale de poissons dans les Grands Lacs et la détermination du pourcentage de cette production nécessaire à la permanence et au rétablissement du système de production de poissons.

Profitant de l'atmosphère détendue qui règne au centre Quetico (nord de l'Ontario), les participants au colloque se sont plongés pendant deux semaines dans les questions liées au métabolisme au sein des communautés et à son rôle dans le maintien, le rétablissement et l'exploitation. Pendant la première semaine, ils ont présenté des cas, ainsi que les développements récents et de nouveaux modèles analytiques dans le domaine de l'écologie terrestre et théorique qui peuvent être appliqués au rétablissement des communautés de poisson des Grands Lacs. La deuxième semaine a été consacrée au tri de ces données fondamentales, aux quelles on a incorporé les tendances principales ou les généralisations obtenues la semaine précédente, et à la rédaction de documents de synthèse. Ce sont ces données fondamentales et ces documents de synthèse qui constituent le compte rendu du colloque.

Le *Journal* fait ses compliments aux participants et aux promoteurs du colloque et il est fier de présenter leurs découvertes et conclusions qui pourront être appliquées à la gestion des pêches dans les Grands Lacs. Le présent supplément du *Journal* est un hommage à tous ceux et celles qui ont joué un rôle dans son organisation, sa production et sa diffusion.

JOHANNA M. REINHART
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Introduction to the International Symposium on Stock Assessment and Yield Prediction (ASPY)[1,2]

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The International Symposium on Stock Assessment and Yield Prediction (given the acronym ASPY) emerged under the sponsorship of the Great Lakes Fishery Commission as another contribution to the efforts of resource management agencies to rehabilitate the degraded fish communities of the Great Lakes. The symposium resulted, in large measure, from almost three decades of nearly continuous progress towards restoration of valuable fishery resources. Once it had become clear that rehabilitation was, in fact, underway in the Great Lakes, a need clearly existed for a better understanding of the factors influencing the rate and direction of the rehabilitation process. The *raison d'être* for ASPY was to enhance understanding of how aquatic production could best be apportioned to maintenance/rehabilitation/surplus production to achieve optimal fishery productivity and benefits for the Great Lakes community.

Background

The achievement of rehabilitation of the 1970s followed decades of uncontrolled loss of fishery resources. Sea lamprey (*Petromyzon marinus*) control was underway everywhere except Lakes Erie and St. Clair, and a multimillion dollar salmonid fishery was developed at a cost for pest control and fish restocking which was a small fraction of the apparent economic benefit. Eutrophication remained a serious impediment to fishery rehabilitation (Colby et al. 1972), but significant reductions in nutrient loadings were being achieved by municipal sewage treatment. While the general pollution problems were still a long way from solution, there had been considerable progress in reduction of both point- and non-point-source loadings to the lakes with significant resultant reductions in fish body burdens of such dangerous contaminants as DDT, PCB, and mercury.

Impressive as water quality improvements had been, the prospects for rehabilitation of the fisheries through reductions of fishing effort and fish community restructuring were even more dramatic, and this was illustrated by the rapid recovery of several depressed stocks. The best examples were the walleye (*Stizostedion vitreum vitreum*) of western Lake Erie and the ciscoes (Coregoninae) of Lake Michigan.

Many of these changes were documented in two earlier international symposia. SCOL (the International Symposium on Salmonid Communities in Oligotrophic Lakes; Loftus and Regier 1972) and PERCIS (the Percid International Symposium; Colby 1977) successfully synthesized the aquatic ecological and fisheries science available in the early and mid-1970's. They focused attention on the general responses of these fish community types to the three principal man-imposed stresses: exploitation, cultural eutrophication, and invasions/introductions of new species. These symposia imposed upon the Great Lakes Fishery Commission and upon cooperating agencies a renewed awareness that ultimate success in rehabilitation of the Great Lakes fisheries demanded a broad approach: one that encompassed control/reversal of all three major man-imposed stresses, one that encompassed the entire fish communities, indeed, an aquatic *ecosystem* approach.

Implications of the Ecosystem Approach

The 1978 U.S.–Canada Agreement on Water Quality was a landmark because it explicitly identified the need for an ecosystem approach to environmental management. At about the same time, two other institutional realignments emerged which reflected similar perceptions about the Great Lakes. An Ontario fisheries study recognized the need for an holistic approach (Loftus et al. 1978) and the product, entitled "A Strategic Plan for Ontario Fisheries", was accepted by the Ontario Cabinet. In the same spirit, in 1981 all the jurisdictions which collaborate together under the aegis of the 1955 International Convention on Great Lakes Fisheries approved the enabling document which called for the preparation of "Strategic Great Lakes Fishery Management Plans." This document explicitly encourages adoption of an ecosystem approach.

Realization of an ecosystem approach included a new appreciation of the ecological role of fish in the Great Lakes. In addition to the traditional view that fishery resources are valuable for human food and recreation, their value as indicators of environmental health was also recognized and has been repeatedly demonstrated by the use of fish to measure the extent of poisonous contaminants in the lakes. An extension of this idea is that loss of resources and distortions in fish community

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[2]Contribution No. 87-17 of the Ontario Ministry of Natural Resources, Research Section, Fisheries Branch, Box 50, Maple, Ont. L0J 1E0.

structure are equally important as integrating measures of the stresses imposed on aquatic systems by human activity.

Renewed awareness of the aquatic ecosystem has been accompanied by discovery of new knowledge about the fish community. The myths of vast fish stocks which were virtually impossible to overfish have been largely dispelled by way of the case histories analyzed in the 1971 SCOL symposium. SCOL also emphasized both the difficulty of isolating the individual effects of concurrent stresses on fish communities and the increasing frequency with which this situation has arisen in recent years.

The SCOL emphasis on community phenomena raised questions about what could reasonably be expected during a rehabilitation or restoration of healthy fish communities in the Great Lakes. Examples of these questions include: What production can be expected from rehabilitated fish communities? What production can the current communities sustain? How can the current "surplus production" be identified, and how can it be apportioned among species, or species groups, to achieve the largest possible safe harvest? How much of the production must be allocated to stock maintenance, and how much more must be left in the lakes to achieve specified rates of rehabilitation? How do we predict what might be safe to harvest in the future? How fast will the rehabilitation proceed? Will rehabilitation be possible, and if so, to what extent?

The urgency of these questions was increasingly apparent as rehabilitation progressed during the 1970s and 1980s. Management agencies were increasingly beset by the sometimes unrealistic expectations of an enthusiastic fishing public. Issues of community structural stability and renewal, fundamental to the very meaning of conservation and long-held concerns of professional biologists, were essentially transparent to the fishing public whose expectations were more closely related to recent levels of fish stocking. Realignments of fishing effort associated with restructuring of fish communities were raising a host of new allocation issues. The more holistic approaches to water quality and fishery management raised issues concerning the relative responsibilities of the general public and the users with respect to sharing the cost of fishery maintenance.

These ecological and social questions, in the absence of previous rehabilitation experience, turned out to be very complex. Similar questions raised in relation to marine fisheries had prompted Gulland (1984) to write "...there is a vital need for...an agreed analysis of the biological conditions of the resource upon which all the national elements in the fishery are based." The breadth of the ASPY challenge precluded in-depth consideration of socioeconomic issues. These became the subjects of another conference (Symposium on Social Assessment of Fisheries Resources; Talhelm 1987) sponsored by the Great Lakes Fishery Commission virtually concurrently with ASPY. The ecological questions forced reexamination of the fisheries models we have been using in the Great Lakes, mostly single-species (exploitation) models. Inevitably such questions underscored the need for new theory applicable to levels of organization above populations or single species, and invited exploration of recent advances in other ecological fields.

Recent Theoretical Developments

Forging new theory has always been a formidable task, and it is reasonable to question the basis for our renewed optimism that the time was right for addressing such complex issues.

It can truly be said that the last 15 yr or so have been the most turbulent and yet productive period in the history of aquatic science in the Great Lakes basin. Critical concerns about pollution brought about substantial advances in physical and chemical limnology (Saylor et al. 1981; Fraser and Robertson 1981). In fisheries, the SCOL and PERCIS symposia were followed by the Sea Lamprey International Symposium (Smith 1980) and the Stock Concept International Symposium (Berst and Simon 1981). These symposia further defined the state of fishery science in the Great Lakes and the trend towards increasingly sophisticated analysis and modeling of large aquatic systems.

A number of theoretical models at the ecosystem level of resolution which are relevant to fish productivity have also emerged recently. Vollenweider (1968) related primary production to nutrient loading. Ryder (1965) and Ryder et al. (1974) generalized the linkage between fish yields and an index (the morphoedaphic index or MEI) encompassing lake morphometry and nutrient loading. Beyond the observation that yield appears to be a conservative system property which is not greatly affected by the trophic levels subjected to fishing, the model is not appropriate to analysis of trophic structure. In this area, the generalization of Sheldon et al. (1972) about the distribution of particle sizes in marine pelagic systems has been usefully advanced by Kerr (1974). There have also been interesting theoretical developments in the area of functional relationships in the trophic hierarchies of fish communities (Dickie 1976).

There have been substantial advances in yield modeling and in control theory for the population level as well. Deriso (1980) and Schnute (1985) have developed robust formulations for characterizing yield changes in marine fisheries. Hill and Durham (1978) have called for the application of control theory in rationalizing the behaviour of aquatic ecosystems. Their discussion of "congeneric homotaxis" should strike a resonant chord with the taxonomic arguments for community stability offered by Smith (1968) for Great Lakes coregonines and by Regier et al. (1969) for the Lake Erie percid community. Botsford (1981) has increased the realism of traditional models based upon physiological energetics by including size, age, and density dependence. His results predict instability from size-selective fishing and depressed equilibrium levels in stocks exhibiting accelerated individual growth rates. Getz (1980) and Levin (1981) dealt with management strategies appropriate to multiple-age spawning stocks. The practical problem of setting limits on harvesting has been addressed in the concept of "vulnerability" articulated by Vincent (1981). Goh (1981) has also attempted to marry the ecological theory of *r*-selection and *K*-selection to management rules directed at exploitation of fishes of differing fecundity.

The ASPY Challenge

The examples above led us to suspect that many of the problems facing Great Lakes rehabilitation efforts might already have been solved in other contexts. We were confident that the recent research activity directed at better predictive models in ecology and fisheries could be focused further toward solution of Great Lakes problems. The challenge for ASPY was to provide conceptual models of fishery dynamics that transcended the unit stock formulations. Equally, these new approaches must deliver cost-effective estimates of the state of variables controlling the process of fish production in complex communities in order to provide management tools for achiev-

ing the productive potential of the Great Lakes. In parallel, we sought indicators for gauging progress toward rehabilitation objectives using models scaled in units reflecting the time necessary for recovery of debilitated fish communities. A final critical requirement was that our conceptual models must allow prediction of the results of management actions, i.e. they must be testable in the real world.

During the inevitable publication lag since the symposium was convened in August 1985, we have been gratified to see the emergence of several important extensions of ideas that were debated at ASPY, and new approaches that reaffirm our conviction that ASPY was both timely and relevant to Great Lakes needs. Recent papers by Fournier and Doonan (1987) and Schnute (1987) significantly strengthen our analytical framework for single-species fisheries. The volumes by Walters (1986), Vincent et al. (1987), and Ulanowicz and Platt (1985) advance the frontiers of knowledge about control of complex biological systems. In the papers that follow, we hope readers will find, as we have, exciting results and new challenges for management and research as fishery rehabilitation progresses during the next few decades.

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Interspecific Relations among Fish Species in South Bay, Lake Huron, 1949–84[1]

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Of the nine species caught in pound and gill nets in South Bay, Lake Huron (lake whitefish (*Coregonus clupeaformis*), rainbow smelt (*Osmerus mordax*), lake trout (*Salvelinus namaycush*), splake (*S. namaycush* × *S. fontinalis*), burbot (*Lota lota*), lake hering (*Coregonus artedii*), alewife (*Alosa pseudoharengus*), white sucker (*Catostomus commersoni*), and yellow perch (*Perca flavescens*)), only yellow perch, white sucker, and lake whitefish were significantly related to the abundances of all other fish species (multiple regression) from 1965 to 1984. For the longer period (pound nets 1949–84), all but smelt, burbot, and white sucker were dependent upon variations in the abundance of the nine other species. For the same period (1965–84) and species (nine), the abundances only of yellow perch and white suckers were significantly and positively related in two basins of the Bay. None of the inverse correlations between species abundances was significant in both basins. Within the Outer Basin, only the correlations between alewife and lake herring ($r = -0.49$, $r = -0.45$) and yellow perch and white sucker ($r = +0.55$, $r = +0.47$) were significant in the same direction for both time periods (1949–64 and 1965–84, respectively). We concluded that there was little evidence that the abundances of species were affected significantly by interspecific influences.

De 1965 à 1984, parmi les neuf espèces capturées au verveux et au filet maillant dans la baie South du lac Huron, à savoir le corégone de lac (*Coregonus clupeaformis*), l'éperlan arc-en-ciel (*Osmerus mordax*), le touladi (*Salvelinus namaycush*), la truite moulac (*S. namaycush* × *S. fontinalis*), la lotte (*Lota lota*), le cisco de lac (*Coregonus artedii*), le gaspareau (*Alosa pseudoharengus*), le meunier noir (*Catostomus commersoni*) et la perchaude (*Perca flavescens*), seuls la perchaude, le meunier noir et le corégone de lac présentaient une relation significative (régression multiple) avec l'abondance des poissons des autres espèces. Dans le cas des prises au verveux de la plus longue période de données disponibles, soit de 1949 à 1984, l'abondance de toutes les espèces à l'exception de l'éperlan, de la lotte et du meunier noir, variait en fonction des variations de l'abondance des neuf autres espèces. Pour la même période (1965–1984) et les mêmes espèces (neuf espèces ci-dessus), seule l'abondance de la perchaude et du meunier noir présentait une relation significative positive dans les deux bassins de la baie. Aucune des corrélations inverses notées entre l'abondance des espèces était significative dans chacun des bassins. Dans le bassin externe, seules les corrélations entre le gaspareau et le cisco de lac ($r = -0,49$, $r = -0,45$) et la perchaude et le meunier noir ($r = 0,55$, $r = +0,47$) étaient significatives et de même orientation pendant les deux périodes (1949–1964 et 1965–1984, respectivement). Les auteurs concluent qu'il y a peu de faits indiquant que l'abondance des espèces ait significativement été modifiée par les influences interspécifiques.

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The aim of the South Bay Experiment (Fry 1947) was to exert equal fishing pressure on all of the species, and thereby test the nypothesis that yields of valuable species would be enhanced if competing coarse fish also were removed. This experiment was ended because the affects of lamprey (*Petromyzon marinus*) and alewife (*Alosa pseudoharengus*) were not anticipated in the original experimental design. However, sampling of the catches from pound nets (1949–84) was continued and new sampling gear was introduced in later years (1965–84).

What factors explained the changes in relative abundances that have occurred since 1949 in South Bay? We focus on two hypotheses: first, interspecific interactions explain a significant portion of the variations in species abundances, and second, the sign and direction of these interspecific correlations of annual relative abundances are the same for the fish communities in the Inner and Outer basins and between two periods of time (1949–64 and 1965–84) in the Outer Basin. It is assumed that inverse correlations of annual relative abundances can be interpreted as evidence for negative interactions between

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species, whereas positive ones indicate that similar factors influence abundances.

These two hypotheses are relevant to the question of the importance of stochastic and deterministic factors to the structure of fish communities (Grossman et al. 1982). The determinists (Grossman 1982) maintain that communities are at equilibrium and that species avoid competition through such means as resource partitioning. In contrast, the stochastic school supports the idea that the environment is unstable, and therefore does not permit an equilibrium state to be achieved. Alternatively, Weins (1977) hypothesized that competition is important but that its influence is sporadic. None of these three hypotheses would predict, necessarily, that interspecific interactions would be evident from correlation analyses of variations of relative abundances in stable communities. However, Goeden (1982) concluded that the removal of keystone predators (Paine 1969) can result in a compositional change in the fish community. In Lake Huron, the loss of the keystone predator (lake trout, *Salvelinus namaycush*) may have effected a compositional change, promoting conditions conducive to competitive crunch (Weins 1977). Thus, if interspecific interactions are important but not normally evident in equilibrium states (Grossman et al. 1982), the period following the loss of lake trout in South Bay (Fry 1953) may have provided an opportunity to determine if interspecific interactions were evident during a period when the biological adaptations (resource partitioning) were disrupted. Furthermore, the presence of exotic species (rainbow smelt (*Osmerus mordax*) and alewife) provided us with the opportunity to assess interspecific interactions between exotic and indigenous species. If these exotic species were simply filling a niche that was temporarily or permanently void (Christie et al. 1972), one would not expect to detect interspecific interactions between exotic and indigenous fish species.

Methods

South Bay (Fig. 1), extending 26 km from Lake Huron into Manitoulin Island, consists of two basins; the larger, deeper one supporting cold-, cool-, and warmwater species (A = 7490 ha; Z = 20.2 m) and the smaller, shallower basin (A = 1361 ha; Z = 7.6 m) maintaining cool- and warmwater species throughout the year, but also serving as a temporary habitat for cold-water species for all but the summer months. From the geographical dstribution of fish species caught and tagged in South Bay, and then recaptured in South Bay and Lake Huron (Henderson et al. 1983; Henderson 1986), it was concluded that the communities in the Inner and Outer basins did not mix appreciably and that the Outer Basin community mixed freely with the assemblage in the adjacent waters of Lake Huron.

The first hypothesis, that interspecific interactions explained a significant part of the variations of species' abundances, was tested by correlating the annual relative abundance (catch-per-unit-of-effort (CPUE)) of each species caught in pound and gill nets with the CPUE of each of the other species caught annually in the respective nets in South Bay. The Outer Basin community was sampled annually from catches in two pound nets set in June and lifted every 3–4 d. The CPUE's derived from the catches in these two nets were pooled because the CPUE's were significantly correlated ($P < 0.05$). Thus, the CPUE is the pooled geometric mean of the number of fish caught, divided by the number of nights that the nets were set in June. The pound net cribs (30-mm-mesh stretched measure) were set at a depth of 10.5 m and the leads were 166 (P4) and 205 (P5) m long. The

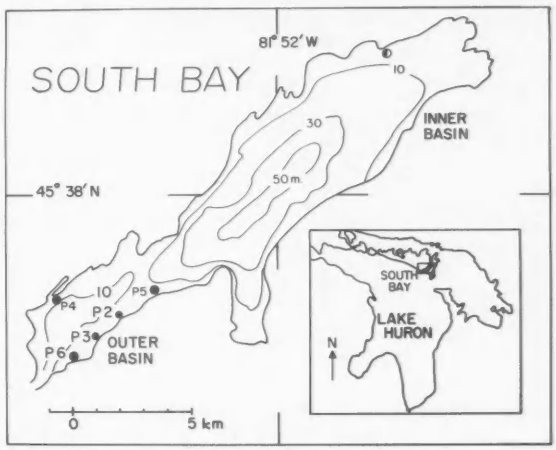

FIG. 1. Location of South Bay sampling gears used to assess the fish community.

annual CPUE derived from the gillnet catches in the Inner Basin is the geometric mean of the numbers caught, divided by the number of standardized gillnet sets. The standardized gill net consisted of ten 138-m panels of 25-, 38-, 44-, 51-, 70-, 76-, 89-, and 112-mm multifilament twine (stretched measure). Usually, 15 one-night sets were made during August at fixed locations from 1965 to 1984. A stepwise multiple regression analysis was done to determine if the abundance of each species was dependent upon the abundance of the other species (Snedecor and Cochran 1967). For all of these analyses, only the most abundant species found in both Inner and Outer basins were used in the analyses (lake whitefish (*Coregonus clupeaformis*), rainbow smelt, lake trout, splake (*Salvelinus namaycush* × *S. fontinalis*), burbot (*Lota lota*), lake herring (*Coregonus artedii*), alewife, white sucker (*Catostomus commersoni*), and yellow perch (*Perca flavescens*)). These species contributed to over 90% of the biomass caught in both gears.

The second hypothesis, that the community structures in the two basins were similar, was tested by comparing the interspecific correlations of CPUE of each species with all of the other species in both basins for the same period (1965–84). In addition, the structure of the community, as shown by the direction and quantity of correlation coefficients, was compared between 1949–64 and 1965–84 in the Outer Basin to see if the community structures changed with time.

We assume that the use of gill nets (Inner Basin) and pound nets (Outer Basin) did not prejudice our comparison of the communities in the basins, for the following reasons. First, we used only those species that were found in both basins, and second, although the catchability coefficients of the gears differed, the CPUE's would be assessed equally well. There is no reason to believe that the catchabilities changed differently for the two sampling devices (gill and pound nets) depending upon the density of the fish species. The size distribution of the species captured in the two gears did not differ sufficiently (both tended to catch larger whitefish, lake trout, splake, burbot, lake herring, white sucker, and yellow perch). Generally, the size distribution of smelt and alewife caught in the two gears was similar enough to preclude the possibility that the gears sampled different populations. Finally, neither type of sampling gear

TABLE 1. Coefficients of correlation between abundances of nine species sampled from gill (d) and pound nets (a, b, c) in South Bay (1949–84) (a = 1949–64, b = 1965–84, c = 1949–84, and d = 1965–84. Significant correlations are $*P < 0.05$.

	Lake whitefish	Rainbow smelt	Lake trout	Splake	Burbot	Lake herring	Alewife	White sucker	Yellow perch
Lake whitefish		−0.36 (d)	−0.45*	0.06	0.02	−0.09	−0.43	−0.50*	0.06
Rainbow smelt	−0.46 (a) −0.16 (b) −0.29 (c)		0.04	−0.34	0.38	−0.18	0.23	−0.07	−0.15
Lake trout	+0.55* 0.35 0.55*	−0.16 0.38 −0.01		−0.03	0.01	0.31	0.22	0.20	0.09
Splake	−0.28 −0.01 −0.17	0.30 −0.03 0.29	−0.36 0.35 −0.20		−0.12	−0.04	−0.06	−0.08	−0.24
Burbot	0.24 −0.44* −0.12	−0.26 −0.24 −0.13	0.29 −0.33 0.15	−0.47* 0.11 −0.18		−0.18	0.22	−0.06	−0.01
Lake herring	0.35 0.15 0.41*	−0.08 0.13 0.10	0.14 0.29 0.31	−0.50* 0.40 −0.29	0.09 −0.26 0.06		0.39	−0.60*	0.53*
Alewife	−0.35 −0.27 −0.31	−0.11 −0.22 −0.08	−0.34 −0.41 −0.26	0.35 −0.20 0.23	0.31 0.30 0.26	−0.49* −0.45* −0.35*		0.68*	0.24
White sucker	0.04 0.22 0.07	−0.37 −0.13 −0.20	−0.21 0.13 −0.11	0.19 −0.18 −0.01	0.24 0.16 0.18	−0.55* −0.28 −0.27	0.57 0.13 0.29		0.48*
Yellow perch	−0.14 −0.23 0.07	−0.36 −0.01 −0.06	−0.28 −0.16 0.06	0.52* 0.35 0.42*	−0.25 0.28 −0.06	−0.40 −0.45* 0.04	0.46 0.67* 0.39	0.55* 0.47* 0.20	

was ever saturated to the point where a preponderance of one species prevented other species from being captured.

Results

Hypothesis 1: Interspecific Interaction and Species' Abundances

In the Outer Basin fish assemblage, when abundances were compared over the entire period from 1949 to 1984, only one significant inverse correlation of abundance was found (lake herring – alewife, $r = -0.35$, df = 34; Table 1); four significant positive correlations were evident. However, all but smelt, burbot, and white sucker were significantly dependent upon the relative abundances of the other eight species (Table 2).

The results were quite different when the two time periods (1949–64 and 1965–84; Table 1) were analyzed separately. In the first period, there were four significant inverse correlations between species (splake–burbot, $r = -0.47$; splake – lake herring, $r = -0.50$; alewife – lake herring $r = -0.48$; lake herring – white sucker, $r = -0.55$; Table 1). None of the species in this period was, however, significantly dependent upon the abundance of the other species (Table 2; multiple regresson). In the second period, three negative correlations were significant (burbot – whitefish, $r = -0.44$; alewife – lake herring, $r = -0.45$; lake herring – yellow perch, $r = -0.45$). One species' abundance (yellow perch) was dependent upon the abundance of the other species (Table 2). For the period from 1965 to 1984, there was only one significant inverse correlation in the Inner Basin (white sucker – whitefish, $r = -0.50$; Table 1), and only whitefish and white sucker were significantly dependent upon the abundance of the other species (Table 2).

These results do not lead unequivocally to the rejection or acceptance of the hypothesis, particularly for the shorter time periods (1949–64 and 1965–84). For the combined period (1949–84), there was much clearer evidence that the abundances of species were significantly related, even if the incidence of significant inverse correlations was rare.

Hypothesis 2: Repeatability of Community Structure

The only consistent correlation between species found in the Inner and Outer basins (1965–84) was between yellow perch and white sucker ($r = +0.48$, $r = +0.47$, respectively). A complete reversal occurred with the relation between yellow perch and lake herring (Inner Basin, $r = +0.60$; Outer Basin, $r = -0.45$; Table 1). The correlation between alewife and lake herring was significantly inverse in the Outer Basin ($r = -0.45$) and positive but not significant in the Inner Basin ($r = +0.39$). In general, there was little consistency between the sign and quantity of correlations between species in the two basins (Table 1), regardless of the significance of the correlations. Correlations of the correlations of CPUE in the two basins were significant only for whitefish, lake trout, and splake ($P < 0.05$, df = 7) in both basins.

Comparing time periods (1949–64 and 1965–84), only two correlations were consistently significant in direction (lake herring – alewife, $r = -0.49$, $r = -0.45$; yellow perch – white sucker, $r = +0.55$, $r = +0.47$, respectively). Regardless of the

TABLE 2. Probability levels of multiple regression of species on all other species in either pound or gill nets in South Bay (1949–84) and the r^2 value (in parentheses) for the significant regressions.

Species	Outer Basin			Inner Basin
	Pound net (1949–84)	Pound net (1949–64)	Pound net (1965–84)	Gill net (1965–84)
Whitefish	0.002 (0.55)	0.22	0.42	0.04 (0.70)
Rainbow smelt	0.10	0.30	0.75	0.09
Lake trout	0.02 (0.46)	0.50	0.23	0.47
Splake	0.01 (0.46)	0.15	0.46	0.89
Burbot	0.32	0.27	0.50	0.49
Lake herring	0.01 (0.48)	0.28	0.64	0.17
Alewife	0.02 (0.45)	0.20	0.11	0.06
White sucker	0.28	0.17	0.43	0.002 (0.83)
Yellow perch	0.01 (0.47)	0.15	0.04 (0.68)	0.42

significance of these correlations of CPUE, all but splakes' and burbots' correlations of correlations of CPUE were significant ($P < 0.05$, df = 7) for the two time periods. Therefore, there was some evidence that, even if the correlation coefficients were not significant statistically, the same pattern of correlations existed between species for two time periods.

Thus, we rejected the hypothesis that the sign and quantity of correlations between species were repeatable between areas (Inner and Outer basins), but accepted the hypothesis that correlations of CPUE persisted from 1949–64 to 1965–84 in the Outer Basin.

Discussion

Although there was some evidence that the abundances of species were dependent upon other species' abundances, in the statistical sense at least, there was little evidence that negative interactions explained much of these relationships between species. However, statistically insignificant inverse correlations were plentiful, and the sum of these could have an accumulative effect on the abundance of species. Normally, one would not expect that a stable community of fish would demonstrate very strong negative interspecific interactions because, first, the resources are partitioned in such a way as to reduce direct competition, and second, predators would maintain prey populations at levels that did not promote competition between species. In South Bay, the loss of the keystone predator (lake trout) would have, in theory, allowed the increase in the abundance of prey species or the colonization of exotics (alewife, smelt) that could have brought about more competition between species. Alewife abundance was inversely correlated with the abundance of lake herring and splake, but smelt did not exhibit any significant inverse relations with other species. The absence of evidence for interrelationships between species may, in part, be a statistical one. When the data were divided into two time periods (1949–64 and 1965–84), the abundances of one species as a function of the other species were not as evident as for the analysis of the combined period (1949–84). It is clear that the evidence for competition, as reflected in inverse correlations of CPUE, was poor, despite the fact that during this time following the loss of lake trout, one expected the most intense expression of competition. The alternative is, of course, that the community was not integrated through interactions between species.

The simplest explanation for the variations in the abundances of four species that account for most of the catch in the Outer Basin may have nothing to do with interspecific interactions. Most of the variation in the abundance of whitefish was explained by the effect of stock size on recruitment and by the action of the commercial fishery (Henderson et al. 1983). Yellow perch recruitment was related to lake levels and was not related to the abundances of other species in South Bay (Henderson 1985). Alewife recruitment and abundance were correlated with water temperatures (Henderson and Brown 1985). Henderson (1986) showed that lamprey parasitism was the cause of fluctuations in the abundance of white sucker. Apparently, the relative importance of species interactions, intraspecific density dependence, water temperature, and lake levels on a species' population dynamics varies spatially and temporally. Thus, it is important to know what conditions would be conducive to competitive interactions. One conclusion is clear from this study: exotic species, such as alewife, show the clearest evidence of interactions with indigenous fish species. The question is, do indigenous species interact within the normal ranges of density and environmental conditions?

The second hypothesis, that the quality and quantity of interspecific correlations between species were repeatable in different geographical locations, was tested by comparing the Inner and Outer basin fish communities (1965–84). Although the magnitude of interactions could clearly vary between communities, at least the sign of the correlations should be the same. If not, changes in community composition of one lake cannot be predicted from an understanding of the interspecific associations of the same species in another lake. Our comparisons of species interactions (correlation) in the Inner and Outer basins showed that there was little consistency in either the magnitude or sign of the correlations. Clearly, other factors influence the interactions between species that cannot be ascertained by simply assessing the changes in the compositions of the community. The sign of the correlations could change if, for example, the ratio of absolute abundances changes; Skud (1982) described this as a change in "dominance." The correlation between whitefish and white sucker abundances was positive in the Outer Basin, but negative in the Inner Basin. We were unable to determine if the dominance was different for these two species in the two basins, but we can infer something about dominance from the physical characteristics of the habitats. Although the pound nets caught fish that frequent the Outer Basin, it was assumed that these catches were samples of the community in Lake Huron connected to the Outer Basin directly. Tagging studies seem to support this assumption for both whitefish and white sucker (Henderson et al. 1983; Henderson 1986). The ratio of the volume of area of habitat suitable for whitefish is lower in the Inner Basin because there is relatively more shallow and warm water in the Inner Basin. In contrast, there is relatively more cold water for the Lake Huron fish community. Thus, one would expect that white suckers are more dominant in the Inner Basin. In conclusion, inconsistencies in the interspecific correlations do not necessarily mean that the correlations are spurious. These inconsistencies between communities at different times and places may have to be evaluated in terms of the differences in the dominance of species or the physical structure of the habitat.

In summary, the main thesis of this study was that interspecific interactions, as shown by correlations of relative annual abundances, can significantly affect the abundance of species. With the available evidence, we could not reject or accept this

hypothesis. The evidence that interspecific correlations differ geographically does not mean necessarily that these correlations are spurious. Other factors such as dominance (Skud 1982), weather, and lake morphology may modify the expression of these interactions between species. Studies of this kind do result in hypotheses about community interactions, but they must be complemented by more detailed studies to explain the mechanisms of interactions.

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Dynamics of the Recovery of the Western Lake Erie Walleye (*Stizostedion vitreum vitreum*) Stock[1,2]

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After its 1957 collapse under intensive fishing and environmental stresses, the walleye (*Stizostedion vitreum vitreum*) stock of western Lake Erie remained low throughout the 1960s. A moratorium on both sport and commercial fishing, resulting from the 1970 discovery of mercury concentrations in walleye flesh, provided an opportunity for the development of an international interagency management plan. The quota management plan developed depended on sequential projection of the fishable stock on the basis of estimated annual recruitment and reports of total withdrawals from the stock. The fishery reopened gradually and quota management (including allocation among jurisdictions) was implemented in 1976. The stock, which had been gradually increasing as a result of relatively strong year-classes produced in 1970, 1972, and 1974, responded well to limited exploitation and produced a record year-class in 1977. Quotas were exceeded in 1978–80, but the stock continued to improve to the extent that the recommended rate of exploitation was increased in 1980 and again in 1981. As the population expanded, growth began to decline; the decline became apparent in young-of-the-year in the early 1970s and in older walleyes in the late 1970s. This trend toward progressively slower growth, which continued in the 1977 and subsequent year-classes, was accompanied by an increase in length at sexual maturity and a decrease in the percentage of female walleyes reaching sexual maturity at age III. As a net result of these changes, the proportion of mature females in the stock (an index of stock fecundity) decreased slightly during the interval 1975–84, while the estimated biomass of the standing stock rose from 9 000 to nearly 26 000 t. Both sport and commercial catches increased markedly after 1980 in Lake Erie's central basin.

Aprés son effondrement de 1957 causé par une pêche intensive et des contraintes environnementales, le stock de doré jaune (*Stizostedion vitreum vitreum*) de la partie ouest du lac Érié est demeuré à un faible niveau tout au long des années 1960. Un moratoire imposé aux pêches sportives et commerciales suite à la découverte, en 1970, de mercure dans la chair des dorés, a fourni l'occasion d'élaborer un plan de gestion international inter-organismes. Ce plan de gestion par contingentement reposait sur une projection séquentielle du stock exploitable elle-même basée sur une estimation du recrutement annuel et sur les quantités totales prélevées signalées. La pêche a été graduellement autorisée et la gestion par contingents (y compris une répartition entre les juridictions) a été établie en 1976. Le stock, dont le volume s'était graduellement accru grâce aux fortes classes annuelles des années 1970, 1972 et 1974, a bien réagi à une exploitation limitée et on a noté une classe annuelle record en 1977. Les contingents ont été dépassés de 1978 à 1980, mais le volume du stock a continué de s'accroître de telle sorte qu'il a été nécessaire d'augmenter le taux d'exploitation recommandé en 1980 et, encore une fois, en 1981. À mesure que la population a pris de l'ampleur, le taux de croissance a commencé à décliner. Ce déclin a été noté chez les jeunes poissons de l'année au début des années 1970, et chez les dorés plus âgés, vers la fin de cette décennie. La tendance vers un taux de croissance à la baisse, que l'on a continué de noter chez la classe annuelle de 1977 et des années suivantes, s'est accompagnée d'une augmentation de la longueur à maturité sexuelle et d'une baisse du pourcentage de dorés femelles atteignant la maturité sexuelle à l'âge III. Ces changements ont eu pour résultat net une légère baisse de la proportion de femelles matures constituant le

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stock (un indice de la fécondité du stock) de 1975 à 1984 bien que la biomasse estimée du stock soit passée de 9 000 t à près de 26 000 t. Les prises tant de la pêche sportive que commerciale du bassin central du lac Érie ont augmenté de façon marquée après 1980.

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The walleye (*Stizostedion vitreum vitreum*) has long been a valuable commercial and sport fish in the western basin of Lake Erie (Fig. 1). Inasmuch as the history of the fishery before 1970 has been reviewed in detail elsewhere (Regier et al. 1969; Parsons 1970; Hartman 1973), our discussion is limited to that information required for an understanding of more recent events. (For the years before 1976, harvest statistics are available only for the commercial fishery; sport catch can only be inferred from scattered survey efforts.) Harvests fluctuated between 334 and 1356 t from 1915 to 1936, falling below 600 t in only four years. Harvest in the western basin began to increase slowly in the 1940s, after the loss of the valuable fishery for lake herring (*Coregonus artedii*), and then rapidly in the 1950s, after the collapse of the blue pike (*Stizostedion vitreum glaucum*) in the central basin (Fig. 2). The catch of walleyes reached a peak of 6975 t in 1956, and more than 6000 t were harvested in 1957. The stock then collapsed and commercial production dropped to only 267 t in 1962, rose briefly to 1119 t in 1963, and fell to a record low of 161 t in 1969.

In 1970, when investigations by the Ontario Water Resources Commission revealed levels of mercury in walleye tissue exceeding the U.S. Food and Drug Administration guideline for food fish (0.5 ppm), the commercial fishery was closed in both United States and Canadian waters of the western basin, and retention of walleyes caught by anglers was prohibited in Ontario and Michigan waters. After 1972, as mercury contamination declined due to a reduction in discharges by the chloralkali industry, the walleye fishery in Ontario was reopened to both sport and (limited) commercial use; in Michigan and Ohio, however, the harvest was restricted to angling.

Recognizing the importance of continued protection of the still depleted resource as the fishery reopened, the Great Lakes Fishery Commission sponsored an international interagency meeting in March 1973 to discuss coordinated management of walleyes in western Lake Erie. This meeting resulted in the formulation of an international plan for conservation and rehabilitation of the walleye resource and recommended the formation of an interagency Scientific Protocol Committee (SPC) to evaluate walleye population dynamics and develop forecasts of abundance. The plan was formally endorsed by the Commission in June 1973 and forwarded to the respective governments in July. The SPC began work in November 1973 and presented its first definitive report in March 1976.

In accordance with the objectives delineated during the March 1973 meeting, the SPC developed a system of quota management for the walleye fishery (methodology is discussed later) involving sequential projection of the fishable stock, conservative exploitation rates to foster recovery of the resource, and sharing of the quota among the several jurisdictions on the basis of lake surface area. Each jurisdiction was to allocate its portion of the quota among user groups within its own waters and be responsible for complete reporting of all withdrawals from the stock and enforcement of its portion of the overall quota. The initial quota recommendation was for 1976, and quota recommendations were issued annually in 1976–85.

While the SPC was conducting its analysis, the sport fishery for walleyes in western Lake Erie expanded rapidly in both Ontario and Ohio waters. Although walleyes had always been prized by anglers, catch rates rarely exceeded 0.1 walleye per angler hour during the 1950s and 1960s (Keller 1964; Sztramko and Paine 1984). Catch-per-unit-effort rose slowly during the early 1970s, and then increased sharply from 0.16 in 1975 to 0.50 in 1976 in Ontario (Sztramko and Paine 1984) and from 0.12 in 1975 to 0.61 in 1977 in Ohio (Baker et al. 1979). Angler interest also expanded rapidly, and increased effort, coupled with high catch rate, resulted in a dramatic increase in estimated sport catch from 111 000 walleyes in 1975 to 2 194 000 in 1977 in Ohio waters alone. The Ontario commercial fishery reopened under a limited permit system in 1974 and expanded under a quota system in 1976. The combined harvest of the three jurisdictions exceeded 2500 t in 1977 and reached nearly 4000 t in 1982 (Fig. 2).

Our objectives are to document the recovery of the walleye stock in the western basin of Lake Erie, with specific reference to the period after the mercury crisis, and to examine changes in population characteristics — especially growth and maturation rates — as the population density fluctuated after 1950. We rely heavily on data furnished to the SPC and its successor, the Standing Technical Committee for Lake Erie, by the natural resource management agencies of Michigan, Ohio, and Ontario and by the U.S. Fish and Wildlife Service.

Quota Management and Stock Recovery

The SPC set as its objective the development of a system of coordinated scientific management of the western Lake Erie walleye fishery that would entail equitable allocation of the total allowable catch (TAC) among jurisdictions and concurrent rehabilitation of the resource (Kutkuhn et al. 1976). To accomplish this task, the committee examined existing methodologies for measuring the standing stock and projecting its annual surplus production, identified basic data requirements in relation to the present and future ability to meet them, and derived a procedure for apportioning surplus yields. By canvassing the management agencies, the SPC pooled all the applicable statistical data known to exist for western Lake Erie walleyes. Matching available information on age composition of the catches with corresponding data on catch and effort in the commercial fishery (the sport fishery was not an important source of mortality before about 1975) led to the conclusion that the interval 1963–69 was the only one for which sufficient data were available to estimate the fishable stock.

Inspection of the final results of the population analysis, representing averages for the five year-classes (1962–66) that could be followed throughout their fishable life spans during the above-defined reference period, left little doubt that the fishery's multigear operation imposed a high collective mortality on

FIG. 1. Lake Erie. Shading indicates the extent of the western basin stock as defined by Kutkuhn et al. 1976.

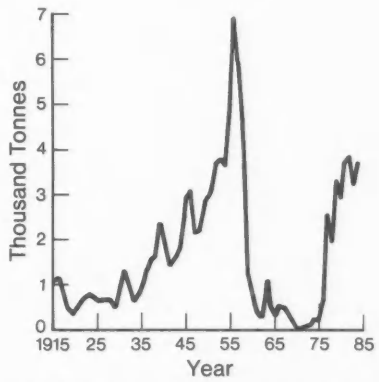

FIG. 2. Reported walleye landings from the western basin of Lake Erie, 1915–1984. Sources: 1915–60, reported catch from Michigan, Ohio, and Ontario listed by Baldwin et al. (1979); 1961–69, catches from Statistical Districts ME, OE-1, OE-2, O-1, and O-2 as reported to the Scientific Protocol Committee (Kutkuhn et al. 1976); 1970–75, commercial catches for OE-1 and OE-2 (Ontario Ministry of Natural Resources 1972a, 1972b, and no date) plus total estimated sport catch; 1976–84, catches reported to the Lake Erie Walleye Task Group annually by each resource agency.

walleyes in western Lake Erie during the 1960s. Total annual mortality in the fishable stock (defined as walleyes older than 1.5 yr) apparently exceeded 90% (Kutkuhn et al. 1976). The obvious result of this heavy pressure on the stock was a significantly attenuated age distribution (catches consisted primarily of walleyes in their second, third, and fourth growing seasons) and greatly reduced reproductive potential.

Establishment of the fishable stock's probable limits of magnitude during the reference period provided a basis for sequential projection of the standing stock into later years (Kutkuhn et al. 1976). A second requirement for sequential projection, an index of annual recruitment during the intervening years, was available in the form of a young-of-the-year (YOY) index based on the catch per hour with a small trawl fished biweekly at seven or more fixed sampling sites from mid-June through October 1959–74 by the U.S. Fish and Wildlife Service (Table 1). The SPC established the relation between the YOY index and the strength of entering year-classes (as judged by their eventual harvest) during the reference period and used this relation to estimate annual recruitment during the interval 1970–76. The third element required for sequential projection — estimates of fishing mortality during the same interval — was necessarily based largely on conjecture. Although the commercial fishery was officially closed from 1970 to 1973, landings of incidental catches were allowed in Ontario. Furthermore, almost no information was available on the extent of mortality inflicted by the increasingly active sport fishery. The SPC assumed, accordingly, that not only did total mortality in the stock drop sharply with closure of the commercial fishery during the "mercury crisis," but that angling mortality had not exceeded about 33% during the 1970–75 interval. (This estimate was subsequently adjusted downward on the basis of scattered creel surveys and their relation to basin-wide surveys conducted after 1975.)

The great innate resiliency of the walleye stock was quickly manifested under the multilateral ban on fishing instituted in the spring of 1970 because of mercury contamination. As indicated by the YOY index, year-classes produced in 1970, 1972, and 1975 roughly equalled the largest produced in the preceding 11 yr, and the 1974 year-class was 40% larger than any of these (Table 1). As estimated by the sequential projection procedure outlined above, the fishable stock at the start of each year (redefined as walleyes of age II and older) increased to 13.8 million in 1976 (Fig. 3). Although the SPC reported in spring 1975 its belief that, despite encouraging signs of improvement, the stock "is still significantly depressed below the western basin's carrying capacity (for this species)," closer examination of the statistical data coupled with field observations led it to suggest in spring 1976 that "the stock actually rebounded more quickly and fully than expected." Thus the stage was set for

TABLE 1. Annual young-of-the-year (YOY) index for walleyes in western Lake Erie. Sources: U.S. Fish and Wildlife Service, 1959–69; Ohio Department of Natural Resources (adjusted to comparability with the USFWS index), 1970–84.

Year	Index	Year	Index
1959	13.2	1972	32.2
1960	0.4	1973	8.3
1961	7.8	1974	36.6
1962	29.6	1975	15.3
1963	1.5	1976	4.3
1964	3.9	1977	105.1
1965	11.1	1978	5.9
1966	0.6	1979	31.0
1967	3.4	1980	81.1
1968	1.7	1981	28.1
1969	5.2	1982	101.6
1970	21.4	1983	0.3
1971	2.0	1984	32.6

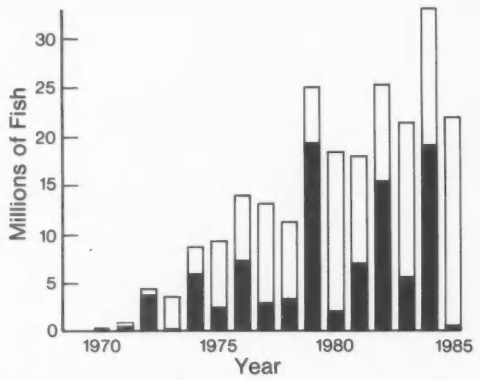

FIG. 3. Fishable stock (numbers) of walleyes in the western basin of Lake Erie at the start of each year, as estimated by sequential projection. The shaded portion of each bar represents recruitment defined as follows: 1970–74, age II walleyes; 1975–78, age II and 10% of the age I walleyes (those age I fish assumed to be vulnerable to the fall fishery (mainly the Ontario commercial fishery)); 1979–85, age II and the number of age I walleyes estimated to exceed 368 mm total length in the fall.

reopening of the walleye fishery under a system of catch quotas to "ensure maintenance of the high productivity to which the stock appears to have been restored" (all quotations from Kutkuhn et al. 1976).

Kutkuhn et al. (1976) noted that "However good the basic data and however acceptable the resulting measure of a stock's size, present assessment techniques falter when attempts are made to ascertain the inertial productivity of that stock." In attempting to meet its goal of allocating surplus production between harvest and rehabilitation, the SPC initially adopted Gulland's (1971) hypothesis that potential sustainable yield is roughly equivalent to half the product of an unfished stock's natural mortality and its virginal abundance. Notwithstanding the less than virginal size of the walleye stock, the TAC for 1976 was recommended on this basis. A slightly different method was used in computing TACs for 1977 and 1978. In this second method, maximum yield was derived from virginal biomass using two ratios: (1) the ratio of size at first capture to maximum size and (2) the ratio of natural mortality to growth (Gulland 1970). Reported landings rose rapidly after the fishery was reopened in 1976 (Fig. 2).

Despite the rapidly increasing harvest, the stock retained its reproductive potential, as evidenced by an extremely strong year-class produced in 1977 (the YOY index for that year was nearly three times higher than that for any year previously reported (Table 1)). When this year-class was recruited in 1979 and 1980, the estimated size of the fishable stock rose to more than double the level of the mid-1970s (Fig. 3). Additional very strong year-classes were produced in 1980 and 1982 when females of the 1977 year-class matured. Recognizing that the stock was still increasing despite 1977–79 landings far in excess of the recommended TACs (Table 2), the Standing Technical Committee recommended and the Great Lakes Fishery Commission's Lake Erie Committee approved doubling the coefficient of fishing (F) used in calculation of TACs from 0.1 to 0.2 effective for the 1980 season. Landings in 1980 again exceeded the TAC (Table 2) without apparent deleterious effects on the stock, and an excellent year-class was produced in 1980 (Fig. 3). Rather than attempt to further limit fishing in the face of still

TABLE 2. Quota allocation and reported catch (thousands of fish) of walleyes in western Lake Erie, 1977–84.

Year and statistic	Jurisdiction			Total
	Michigan	Ohio	Ontario	
1977				
Quota[a]	80.2	477.4	353.4	911.0
Catch	42.0[b]	2194.0	401.7	2637.7
1978				
Quota[a]	54.0	322.0	238.0	614.0
Catch	44.0	1652.0	448.0	2144.0
1979				
Quota	207.0	1230.0	911.0	2348.0
Catch	89.4[c]	3350.8	748.9	4189.0
1980				
Quota	261.7	1558.6	1154.1	2974.4
Catch	183.1	2202.6	1158.1	3543.8
1981				
Quota	367.4	2187.9	1620.0	4175.3
Catch	117.9	2906.8	1312.3	4337.0
1982				
Quota	504.1	3001.7	2222.7	5728.5
Catch	75.7	3048.6	1746.2	4870.5
1983				
Quota	572.0	3406.0	2522.0	6500.0
Catch	85.0[c]	1838.0	1771.2	3694.2
1984				
Quota	676.5	4028.4	2982.9	7687.8
Catch	168.8[c]	3908.6	2287.0	6364.4

[a]Revised quota values based on corrected catch data for 1976–78.
[b]Estimated catch (no report from Michigan).
[c]Estimated by proportion from the Ohio private boat anglers.

apparently increasing abundance, the Lake Erie Committee recommended raising the value of F to 0.285 (an exploitation rate of 22.4%), a value near the top of the optimal range suggested by Shuter and Koonce (1977) for this stock. This value was used in determining the TACs for 1981–83. The 1981 TAC was only slightly oversubscribed, and the 1982 and 1983 TACs (5.7 and 6.5 million, respectively) were not exceeded (indeed, the 1983 catch did not even approach the TAC (Table 2)).

Faced with an estimated fishable stock of 32.8 million walleyes in spring 1984 and increasing evidence that the stock might be approaching the basin's carrying capacity (see later discussion), the Lake Erie Standing Technical Committee's Walleye Task Group recommended that the estimated fishable stock be maintained between 20 and 25 million walleyes by using the following guidelines:

(1) When the estimated fishable stock of two successive years combined falls between 40 and 50 million walleyes, the assigned coefficient of fishing for the next year's TAC computation will be $F = 0.285$.

(2) When the estimated fishable stock of two successive years combined exceeds 50 million walleyes, the coefficient of fishing will be adjusted upward from $F = 0.285$ by appropriating one half of the surplus above 50 million to the first-year TAC.

(3) When any one of the estimated fishable stocks in two successive years is estimated to fall below 20 million walleyes, the coefficient of fishing will be according to the following schedule: 15–20 million walleyes, $F = 0.20$; 10–15 million walleyes, $F = 0.15$; 10 million walleyes, $F = 0.10$.

These recommendations were presented to the Standing Technical Committee and adopted for the preparation of the 1984 and 1985 TACs.

Fluctuations in Growth and Maturity

The heavy fishing pressure of the 1950s drastically altered the age composition of the walleye population in the western basin. Although this stock had apparently always been subject to considerable variation in year-class strength (Deason 1936), disappearance of the older age-groups was pronounced as the fishing-up process proceeded. During 1943–48, an average of almost 20% of the walleyes in samples from the fall trap-net fishery were age IV or older; this proportion dropped to 10% in 1949–55 and to only slightly more than 5% in 1956–61 (Parsons 1970).

This decrease in average age was accompanied, however, by an increase in average size of walleyes in the commercial catch. During 1943–54, walleyes in fall samples averaged 366 mm in total length and 0.45 kg in weight; comparable figures for the 1955–62 period were 406 mm and 0.74 kg (Parsons 1970). Net-run samples taken from commercial trap nets at Sandusky, Ohio, in fall provided the longest series of data for the study of size at age; fall samples also avoid the possibility of bias associated with sexual differences in behavior and distribution associated with the spring spawning season. We grouped the observations into 3-yr segments to avoid the difficulties associated with small samples of certain ages resulting from differences in year-class strength, and here consider only the ages for which sample sizes were sufficient in all time intervals (Fig. 4).

As harvests increased during the 1940s and the larger and older walleyes were removed from the population, the mean

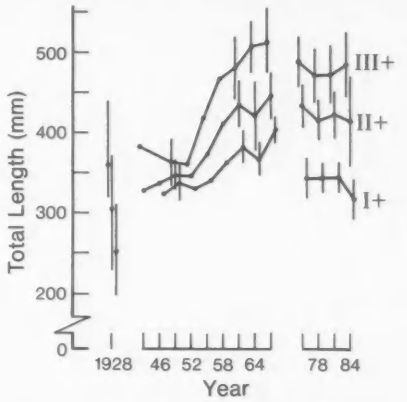

FIG. 4. Mean length of western basin walleyes at the end of their second, third, and fourth growing seasons. Each point represents the mean length in net-run samples from commercial trap nets in three adjacent years. Vertical bars indicate one standard deviation above and below the mean (range for the 1927–29 samples) for the samples for which it could be determined.

length of age III fish seemingly decreased. At the same time, mean length of age I and II walleyes began to increase (Fig. 4), at least partly as a result of reduced intraspecific competition. This increase was reflected in the mean size at age III beginning in 1955. Growth of all age-groups remaining in the population continued to increase sharply after the mid-1950s and was fast enough so that most fish became vulnerable to the fishery almost simultaneously and there was little selection for the faster growing fish. By fall 1960 (after the stock's collapse), the mean size of age I walleyes roughly equalled the mean length of age III walleyes in the mid-1940s (Parsons 1970). Growth rate continued to increase during the 1960s (Wolfert 1977) and mean length at age remained high, although not without some fluctuations, throughout the period of low population abundance (Fig. 4).

By 1968, abundance had become so low that no samples were available from fall trap-net catches (almost the entire season's catch was landed before the end of June as each entering year-class was harvested as soon as it became vulnerable), and there was no fishing during the moratorium resulting from the "mercury crisis." Trawl samples of YOY walleyes taken in fall provide some information to bridge the latter part of this gap (Muth and Wolfert 1986). First-year growth was nearly constant during the 1960s, when the stock was depressed, but declined progressively (Fig. 5) from the early 1970s as stock abundance increased gradually and then rapidly (Fig. 3).

Fall trap-net samples became available again in 1974 and it was immediately obvious that the decline in growth of YOY walleyes had been reflected in age I fish as well (Fig. 4). Length at age declined more slowly in age II walleyes and changes were inconsistent in age III fish, probably as a result of sexual differences in growth and varying representation of sexes in the samples. Muth and Wolfert (1986) examined these declines in detail on a year-by-year basis; here we examine the relation between year-class growth and year-class abundance. One method of doing so is to compare von Bertalanffy growth parameters by year-class. Following the methodology suggested by Gallucci and Quinn (1979), we include comparisons based on the product $K \cdot L_\infty$. The data set contains eight year-classes for which these parameters can be estimated on the

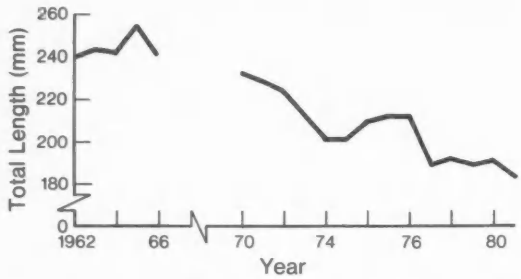

FIG. 5. Mean length of YOY western basin walleyes collected in fall by bottom trawl off East Harbor, Ohio, smoothed by a moving average over 3 yr.

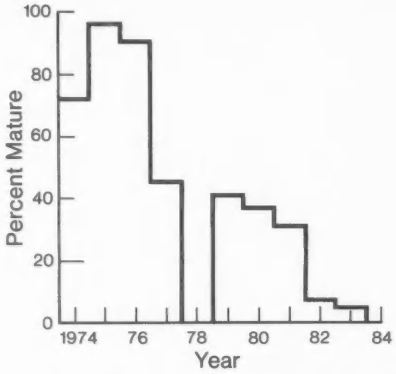

FIG. 6. Percentage of age II+ walleyes that were mature in net-run samples from commercial trap-net samples (sample size was insufficient in 1978).

TABLE 3. Growth coefficients for the 1974–80 year-classes of walleyes in western Lake Erie, derived from fall trap-net samples of fish completing their first through fifth growing seasons (95% confidence limits in parentheses).

Sex and year-class	K	L_∞	$K \cdot L_\infty$
Males			
1973	0.75 (0.25)	502 (32)	377
1974	0.50 (0.17)	529 (45)	265
1975	0.72 (0.02)	477 (3)	343
1976	0.75 (0.25)	478 (29)	358
1977	0.49 (0.21)	515 (56)	252
1978	0.42 (0.16)	552 (63)	232
1979	0.44 (0.35)	579 (142)	255
1980	0.40 (0.41)	591 (200)	236
Females			
1973	0.35 (0.08)	693 (61)	243
1974	0.53 (0.13)	566 (38)	300
1975	0.45 (0.14)	600 (59)	270
1976	0.55 (0.10)	559 (26)	307
1977	0.41 (0.15)	597 (69)	245
1978	0.32 (0.11)	672 (90)	215
1979	0.45 (0.14)	611 (60)	275
1980	0.34 (0.14)	707 (116)	240

basis of length at the end of the first through fifth growing seasons (ages 0 through IV) to assure comparability (Table 3). A sharp decrease in the parameter K and a concomitant increase in L_∞ was apparent in male walleyes, beginning with the 1977 year-class (the first extremely large year-class). The pattern in the female components of the same year-classes is less clear. No trend is obvious in either K or L_∞, but the product $K \cdot L_\infty$ shows a slight downward trend — albeit less pronounced than that for males. We offer no explanation for the apparent inconsistency of results from the 1974 year-class; this year-class had the highest YOY index of any between 1959 and 1977 (Table 1).

Weight at age followed a pattern similar to length at age, but with more variation, and condition factors fluctuated during 1964–83 (Muth and Wolfert 1986). The condition factor of yearling walleyes declined slowly and somewhat erratically from 1976 to 1980 and then declined abruptly from values between 0.96 and 0.99 to 0.91 in 1982 and 0.82 in 1983. Values for age II and III walleyes were also lower in 1983 than in previous years (although not as much lower as those for age I); however, the condition factor for age IV fish remained at roughly its average value.

No observations are available on weight or condition factor of YOY walleyes, but the sum of the above observations indicated that depressed growth in the first two growing seasons began in 1977–78 and that the effects were progressing through the population, at least until the fish attained a relatively large size. These conclusions imply increased competition for food at the abundance levels projected for 1977 and later, and that this competition is not overcome until fish become large enough to consume rather large prey.

Size and age of walleyes at the onset of sexual maturity also changed markedly in the western basin stock (Muth and Wolfert 1986). Females matured at a greater length in the 1980s than in the 1960s and 1970s, and the increase in length at maturity was much more pronounced in males. Age at maturity also changed during the recovery period for both sexes. We concentrate our discussion on changes in females because the abundance of mature males is rarely a limiting factor in fish populations. During 1964–66, 86.3% of the age III females were mature in spring (Wolfert 1969); however, anticipated maturity of fall-caught age II females decreased markedly in 1977 (after fluctuating between 1974 and 1976) and again in 1982 (Fig. 6) to levels below 10%. Sexual maturity of age IV walleyes remained unchanged. Nearly all age IV walleyes (98.6%) examined in 1964–66 were mature (Wolfert 1969), and in recent years, fall-caught age III females exhibited 100% anticipated maturity except in 1974 and 1983 when the proportion dropped to 87.5 and 94.4%, respectively.

Effects of Fluctuations on Stock Fecundity

Decreases in growth and increases in age at maturity may compensate for increases in abundance. To evaluate the net effects of increasing abundance (Fig. 3), decreasing size at age (Fig. 4 and 5), and increasing average age at maturity, we estimated the total biomass of the standing stock at the beginning of each year between 1975 and 1984 (the lack of samples between 1970 and 1974, noted above, precluded estimation for that period), using the sequentially projected stocks for numerical abundance and mean weight in the fall trap-net samples (assuming no overwinter growth), and similar-

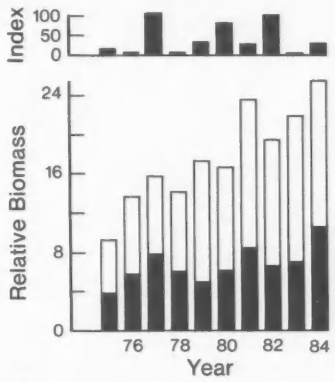

FIG. 7. Annual YOY index (top) and relative biomass of the standing stock of walleyes in the western basin of Lake Erie at the beginning of each year, 1975–84. The shaded portion of each bar represents the proportion of mature females in the estimated standing stock.

ly estimated the biomass of mature females before spawning in the same year. The estimated standing stock increased (with some fluctuations) from 17 to nearly 45 million walleyes and from 9200 to over 25 000 t between 1975 and 1984 (Fig. 7). The estimated biomass of mature females constituted 28–49% of the stock, with values above 40% characteristic of the late 1970s and values near 35% typical of the early 1980s.

Although the large biomass of mature females in 1977 produced a record year-class (as indicated by the YOY index (Table 1; Fig. 7) for that year and by the harvest in 1979 and later years), the higher spawning biomass of 1981 did not produce a notably large year-class, and the 1982 year-class — the second largest since 1959 (as judged by its YOY index) — was produced by a rather average-sized biomass of mature females. The lack of correlation between biomass of spawning females and strength of year-classes produced (Fig. 7) provides further support for the hypothesis of Busch et al. (1975) that environmental conditions during incubation are more important than the size of the spawning stock in determining the success of a year-class. This observation does not contradict the existence of a stock–recruitment relation, however. Shuter and Koonce (1977) demonstrated such a relation after extracting the effects of rate of water temperature increase in the spring. The success of the 1984 spawning by the largest projected biomass of mature females yet recorded (the net result of the size achieved in 1984 by the survivors of the 1977 year-class and full maturation of the 1980 year-class) has yet to be fully evaluated, but the YOY index was only average for the period beginning in 1972. In contrast, the average biomass of spawners in 1983 produced the smallest year-class (as judged by YOY index) since indexing began.

Increasing Abundance in the Central Basin

Although Lake Erie's central basin had contributed up to 25% of Ontario's commercial landings during the 1950s, landings in Ohio did not exceed 5% of the western basin catch, and angling pressure was also light (Keller 1964). Landings from the central basin collapsed simultaneously with those from the western basin. The recovery was not simultaneous in both basins, however; Regier et al. (1969) suggested several reasons for continued low levels of walleye abundance in the central basin, including altered limnological conditions, pollution in spawning streams, siltation of lake spawning grounds, increasing populations of rainbow smelt (*Osmerus mordax*), and a continuing small-mesh gillnet fishery for yellow perch (*Perca flavescens*).

In the Canadian waters of central Lake Erie, catches of walleyes made a noticeable contribution to the 1980 commercial landings and this contribution continued to rise through 1983. A catch of over 4 t in 1983 was attributable to a combination of greater abundance of walleyes and increased effort directed at that species. Sport catches also increased in both Ontario and Ohio waters of the central basin during the 1980s. Results from a 1984 salmon derby in Ontario showed a ratio of one walleye to three coho salmon (*Oncorhynchus kisutch*) harvested; walleyes were rare (1 per 50 fishing trips) in a comparable survey in 1982 (J. Paine, Ontario Ministry of Natural Resources, Wheatley, Ont., pers. comm.). The sport catch from Ohio waters of the central basin increased from 56 000 walleyes in 1982 to 1 million in 1984 (creel survey estimates). Estimated catch rates were 0.12 per angler hour in 1975 and 0.47 in 1984 (Ohio Department of Natural Resources 1985).

The increasing abundance of walleyes in the central basin may be a result of dispersal from the western basin or establishment of a reproducing population in the central basin. Timmerman and Dunlop (1985) reported that walleyes appeared to experience some degree of reproductive success in the western portion of the central basin (vicinity of Erieau, Ont.) as evidenced by the presence of mature, then spent, adults in May, larval walleyes in May, and juveniles in July. Although concentrations of mature, then spent, adults were observed as far east as Plum Point, no confirmation of survival was obtained east of Port Glasgow (81°35′ W longitude). The paucity of prime spawning substrates on both shores of the central basin leads to the speculation that major contributions to the walleye population are unlikely from these areas. This speculation is supported historically — walleyes were abundant outside the western basin only when walleye populations were strong within the western basin (e.g. in the 1950s).

The unanswered question of when (at what life-history stage) movement to the central basin occurs (if it does) has important implications in management of the stock. If the movement is a passive drift of larval walleyes, which are now much more abundant than they were in the 1960s and early 1970s, the present system of establishing quotas for the western basin remains satisfactory. If, on the other hand, the movement is an active migration of yearling and older fish responding to competitive pressures after the YOY index has been established, the central basin catch must be considered a withdrawal from the western basin stock, and taken into account as subsequent projections of fishable stocks and annual quotas are made.

Acknowledgements

Preparation of this report would have been impossible without the data base established by the Scientific Protocol Committee and supplemented since 1976 by annual reports to the Lake Erie Standing Technical Committee by the natural resource management agencies of Michigan, Ohio, and Ontario; we extend our sincere thanks to the many biologists and vessel crewmen who aided in the collection of what may be one of the most nearly complete data sets available for the study of the recovery of a severely depressed fish population.

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Lake Superior Revisited 1984[1]

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The Lake Superior fish community has changed substantially since the early 1960s, when control of the sea lamprey (*Petromyzon marinus*) became effective. Self-reproducing stocks of lake trout (*Salvelinus namaycush*) have been reestablished in many inshore areas, although they have not yet reached pre-sea lamprey abundance; offshore lake trout are probably at or near pre-sea lamprey abundance. Stocks of lake whitefish (*Coregonus clupeaformis*) appear to have fully recovered; commercial catches are at or above historical levels. Lake herring (*Coregonus artedii*) are recovering rapidly in U.S. waters and are abundant in western Canadian waters. The population of rainbow smelt (*Osmerus mordax*), which declined in the 1970s, is recovering. Pacific salmon (*Oncorhynchus*) are becoming more abundant as a result of increased stocking in U.S. waters and are reproducing in most suitable tributaries; they have become significant in anglers' creels.

Depuis le début des années 1960, la communauté piscicole du lac Supérieur a nettement changé suite à la lutte efficace contre la lamproie marine (*Petromyzon marinus*). Des stocks autonomes de touladi (*Salvelinus namaycush*) ont été rétablis dans de nombreuses régions côtières quoiqu'ils n'aient pas encore atteint le niveau d'abondance observé avant les ravages de la lamproie marine. Dans les eaux hauturières, le touladi a probablement atteint son ancien niveau d'abondance. Il semble que les stocks de grand corégone (*Coregonus clupeaformis*) se soient complètement rétablis; les prises commerciales se situent aux niveaux historiques ou à des niveaux supérieurs. Dans les eaux américaines, le cisco de lac (*Coregonus artedii*) se rétablit rapidement tandis qu'il est abondant dans les eaux canadiennes orientales. La population d'éperlan arc-en-ciel (*Osmerus mordax*), dont l'abondance avait diminué pendant les années 1970, se rétablit. Les saumons du Pacifique (*Oncorhynchus*) deviennent plus abondants par suite d'un plus grand effort d'ensemencement dans les eaux américaines et se reproduisent dans les tributaires les plus adéquats. On les retrouve plus fréquemment dans les relevés de la pêche sportive.

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We here review changes in the Lake Superior fish community that occurred in 1970–84, the period following that treated by Lawrie and Rahrer (1972, 1973) in their case history of Lake Superior for the Symposium on Salmonid Communities in Oligotrophic Lakes (SCOL) (Loftus and Regier 1972). That symposium focused on the effects of three major types of stress on the fish communities: exploitation, introductions, and cultural eutrophication. Lake Superior was chosen as an example of a lake that was subjected to exploitation and introductions, but not to eutrophication (Loftus and Regier 1972).

Lawrie and Rahrer (1972, 1973) concluded that overfishing and the invasion of the sea lamprey (*Petromyzon marinus*) were the causes of the major changes in the fish populations up to about 1960. They stated that "overfishing has occurred at some stage, at least, in the decline of every major species," and although not disputing the profound effect of the sea lamprey invasion, they further concluded that "under prevailing management policies exploitation alone would eventually have led to the same result."

The effects of sea lamprey predation on lake trout (*Salvelinus namaycush*) were reflected in the rapid decline of lake trout harvests during the period 1953–62. Thereafter, lake trout abundance increased as a result of the sea lamprey control program of the Great Lakes Fishery Commission (GLFC), lake trout stocking, and near total elimination of exploitation except for assessment purposes. Lawrie and Rahrer (1972, 1973) concluded that, although some shallow-water species may have been adversely affected by sawdust and other woody allochthonous material in the past, and water quality had been degraded in a few localities by domestic, mine, and pulp mill effluents, "there is no suggestion that changes in fish stocks were related to abiotic environmental parameters."

We review the current status of introductions and exploitation and discuss one stress factor — contaminants — that received little mention by Lawrie and Rahrer (1972, 1973). We then document the current conditions of fish stocks in Lake Superior and describe, where possible, the factors that might have led to those conditions. We sometimes include data series

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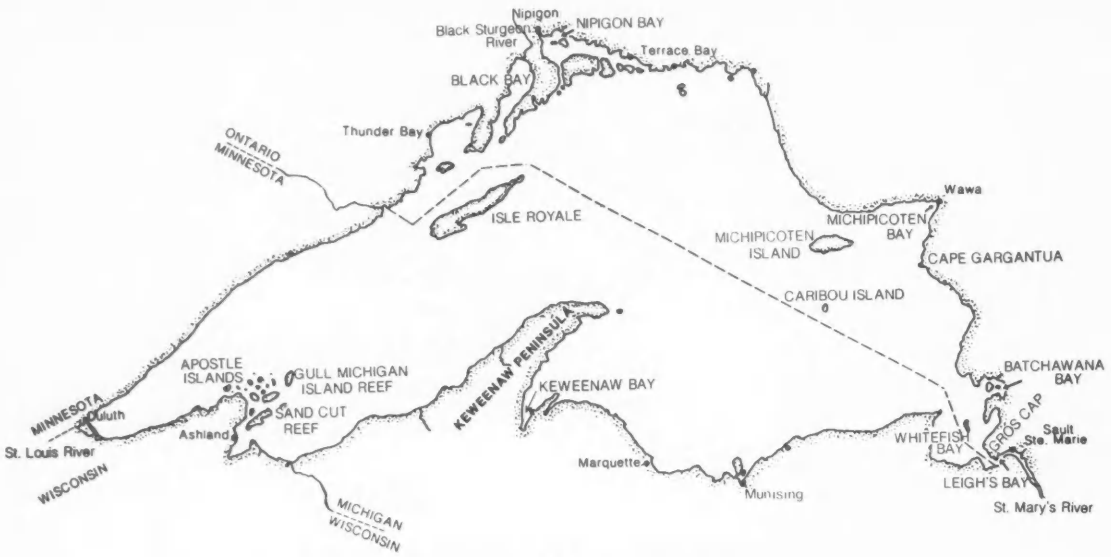

FIG. 1. Lake Superior, showing locations of particular interest in the present work.

that began earlier than 1970 when such inclusion helps to demonstrate a trend. Many of the data sets used are from preliminary or unpublished internal reports of the various state, provincial, and tribal management agencies and the National Fisheries Center – Great Lakes (NFC-GL), of the U.S. Fish and Wildlife Service. We drew heavily on annual reports of the GLFC and on minutes of the annual meetings of the Lake Superior Committee of GLFC. The morphology, morphometry, productivity, and history of Lake Superior were treated by Lawrie and Rahrer (1972, 1973) and Munawar (1978).

Contaminants

Because relatively little was known about contaminants in Lake Superior fishes by the early 1970s, the subject was not discussed by Lawrie and Rahrer (1972, 1973). Currently, various contaminant levels in fish are monitored annually by the U.S. Fish and Wildlife Service and the U.S. Environmental Protection Agency in U.S. waters and by the Department of Fisheries and Oceans and the Ontario Ministries of Natural Resources and the Environment in Canadian waters. The International Joint Commission has also maintained a contaminants surveillance program in Lake Superior, which was intensified in 1983 as part of a Great Lakes International Surveillance Plan.

Most contaminant concentrations have been low enough to pose no apparent threat to consumers or to the fisheries, but there have been a few exceptions. During contaminant monitoring in 1971, high mercury concentrations were detected in Thunder Bay, Ontario (Fig. 1), that were due to effluents from a chlor-alkali plant and paper mills. The local fishery for lake trout was closed in August 1971 and remained closed throughout 1972 and 1973. In a second incident, the commercial fishery operators of eastern Canadian Lake Superior were informed in May of 1978 that unacceptably high PCB levels were present in lake trout designated as siscowets (*S. n. siscowet*) — "fats"; typically deepwater fish with high fat content — and that these fish could no longer be sold in the United States. The sale of siscowets has been banned from all of Canadian Lake Superior since 1978. In general, levels of contaminants in Lake Superior do not appear to have adversely affected fish populations and have affected the fisheries only slightly. Recent information on contaminant concentrations in fish from U.S. waters was given by Clark et al. (1984), DeVault et al. (1985), Lowe et al. (1985), and Schmitt et al. (1985); for Ontario, such information is published annually in a *Guide to Eating Ontario Sport Fish* (e.g. Anonymous, 1985).

Introductions

Sea Lamprey

Details of the invasion and spread of the sea lamprey in Lake Superior and of its effects on the native fishes were presented at the Sea Lamprey International Symposium (Smith 1980) and are treated only briefly here, although sea lamprey predation is still considered to be a major cause of high lake trout mortality (Pycha 1980; Swanson and Swedberg 1980; Koonce and Pycha 1985). Chemical control of the sea lamprey was begun in 1958–60 and remains the most effective means known to reduce sea lamprey numbers. Since the 1980 symposium, two workshops have been sponsored by GLFC, one addressing the interaction of sea lamprey and lake trout (Koonce et al. 1982) and the other examining the effects of integrated sea lamprey control and alternative methods of reducing sea lamprey's abundance and its effects on lake trout (Spangler and Jacobson 1985). Recently, barrier dams have been constructed on several streams, and field trials of the technique of releasing sterilized males will probably soon begin. It is hoped that the development of alternative control methods will reduce dependency on chemicals, as well as further reduce the sea lamprey population.

Salmonids

Although rainbow trout (*Salmo gairdneri*) and brown trout (*Salmo trutta*) have been present in Lake Superior as reproducing populations since the late 1900s, Pacific salmon (*Oncorhyn-*

TABLE 1. Numbers (thousands) of various salmonids stocked in Lake Superior in 1958–82.

Year	Lake trout	Exotics							Grand total
		Splake[a]	Coho salmon	Chinook salmon	Atlantic salmon	Rainbow trout	Brown trout	Total	
1958	987							0	987
1959	668							0	668
1960	1050							0	1050
1961	1260							0	1260
1962	1853							0	1853
1963	2311							0	2311
1964	2631							0	2631
1965	1947					23	27	50	1970
1966	3279		192			325	1	518	3796
1967	3290		467	33		73	26	599	3863
1968	3376		382	50		180	3	615	3988
1969	2827		656	50		395	14	1115	3928
1970	2874		649	150		232	105	1136	3905
1971	2017	13	617	252		223	103	1208	3122
1972	2106		297	472	20	248	109	1146	3143
1973	1905	5	135	509	20	279	128	1076	2853
1974	2093	20	529	523		141	127	1340	3306
1975	2212	15	275	253		314	246	1103	3069
1976	3010	18	400	493	9	445	88	1453	4375
1977	2381	26	627	254		315	133	1355	3603
1978	2461	81	140	478	37	225	103	1064	3422
1979	2403	183	200	501	0	384	131	1399	3671
1980	2409	173	350	729	8	656	90	2006	4325
1981	2679	190	227	362		150	83	1012	3608
1982	2835	168	236	1313	18	1048	83	2866	5618

[a]Lake trout × brook trout hybrid.

chus sp.) are relatively new to the lake. Five species of exotic salmonids, as well as the hybrid splake (lake trout × brook trout, *Salvelinus fontinalis*), have been stocked in nearly every year since 1965 (Table 1). The total numbers of exotic salmonids planted have increased from 50 000 in 1965 to nearly 3 million in 1982. In addition, all introduced salmonids except probably splake and Atlantic salmon (*Salmo salar*) are reproducing in streams tributary to Lake Superior. The amount of natural reproduction of exotic salmonids is unknown but is believed to be large.

Reproducing populations of one or more (up to four or five) species of exotic salmonids occur in most suitable streams and rivers tributary to Lake Superior. In addition to the salmonids deliberately stocked, the pink salmon (*Oncorhynchus gorbuscha*) was accidentally introduced into a stream tributary to Thunder Bay, Ontario, in 1956 (Schumacher and Eddy 1960). Its perpetuation and population expansion during the 1960s and 1970s was clearly a result of natural reproduction. The populations of pink salmon expanded considerably in the 1970s (Kwain and Lawrie 1981; Wagner and Stauffer 1982), and even-year spawning populations resulted from the spawning of 3-yr-old fish (Kwain and Chappel 1978; Wagner and Stauffer 1980). As judged by observations of spawning runs in 1980–84, populations of pink salmon have considerably declined since 1980.

Other Fishes

Several other species are present in Lake Superior as a result of deliberate or inadvertent introductions or of invasions. The introduction and dispersal of rainbow smelt (*Osmerus mordax*) in the Great Lakes was described by Van Oosten (1937), and its present status is discussed later. Five species are dispersed in relatively small numbers, generally in warmwater areas of which specimens have recently been reported from Lake Superior: alewife (*Alosa pseudoharengus*), common carp (*Cyprinus carpio*), fallfish (*Semotilus corporalis*), white bass (*Morone chrysops*), and longnose gar (*Lepisosteus osseus*). Of these several species, only the rainbow smelt appears to have become sufficiently abundant to affect the fisheries and possibly the fish community.

Exploitation

Commercial Fishing

Lawrie and Rahrer (1972, 1973) painted a rather depressing picture of Lake Superior's fisheries in describing the declining and collapsing stocks and concluded that overfishing was implicated in virtually all of these losses. They suggested that improvements in gear (e.g. conversion from cotton to nylon gill nets) and equipment outpaced the management system which typically controlled the fishery by the establishment of closed seasons and limits on fish sizes and the amounts of gear allowed. They also concluded that detection of the depletion of stocks was masked by gear improvements and the sequential depletion of stocks.

Since the decimation of the major commercial fish stocks by

the sea lamprey in the late 1950s, much more restrictive measures have been placed on the commercial fishery as part of the program to rehabilitate the fish stocks in Lake Superior.

Ontario introduced individual quota management in 1984. Each commercial operator was allocated a portion of the estimated allowable catch of each species in the zones for which he was licensed. This step was the most recent in a process that started in 1962 with the introduction of zone quotas for lake trout and included zone quotas for all major species beginning in the mid-1970s. Most fish are taken from Ontario waters by gill nets, although lake herring (*Coregonus artedii*) have also been taken in trawls.

Minnesota has allowed no large-mesh (>114 mm, stretched measure) gillnet fishery since 1962. Lake trout are taken commercially only in an assessment fishery conducted under special permit. Small-mesh (57- to 70-mm mesh) gill nets are regulated by a "limited entry" policy and by a limit on the total amount of net that can be fished for herring and deepwater ciscoes (*Coregonus* sp.). There has been a closed season for lake herring in November since 1973 to protect spawners.

Wisconsin waters have been divided into three types: commercial fishing areas in which catches are limited by quotas, areas restricted to sport fishing only, and refuges in which no fishing is allowed. Lean lake trout have been managed on an individual quota system for state-licensed commercial operators since the late 1960s. The lake whitefish (*Coregonus clupeaformis*) fishery is controlled by a minimum mesh size (>114 mm), a minimum size limit (>432 mm), and closed fishing season during October and November. The deepwater cisco fishery is controlled by limits on mesh sizes and on locations where fishing is permitted.

Michigan completed a program in 1974 to convert the commercial fishery to impoundment gear, and since then there has been no state-licensed inshore large-mesh gillnet commercial fishery, except for a closely controlled lake trout assessment fishery. The impoundment gear, mainly trap nets, are set for lake whitefish, in a fishery controlled by the amount of gear permitted. Total allowable catches are calculated for lake whitefish in all management zones, and about 50% of these, in appropriate areas, are allocated to the various tribal fisheries. A large-mesh quota-controlled gillnet fishery for offshore lake trout (siscowets) is licensed for the waters around Isle Royale and south of Caribou Island. A quota-controlled small-mesh gillnet fishery restricted to water depths greater than 110 m is permitted for deepwater ciscoes and lake herring (lake trout caught in the nets can be sold).

Two Native American groups participate in the management of commerical fishing in Lake Superior: The Chippewa–Ottawa Treaty Fisheries Management Authority in Sault Ste. Marie, Michigan, represents the Sault and Bay Mills bands; and the Great Lakes Indian Fish and Wildlife Commission in Odanah (near Ashland), Wisconsin, represents the Red Cliff, Bad River, Grand Portage, and Keweenaw Bay bands. Both groups conduct assessment and research on fish populations and formulate regulations for enactment by appropriate tribal regulatory groups. The regulations include quotas for each zone and for individual operators, closed seasons, fishing effort limits (length of gill net) for individuals and zones, and boat restrictions (numbers and size).

Sport Fishing

Sport fishing, like commercial fishing, declined drastically during the 1960s and remained insignificant until the lake trout fishery and especially the Pacific salmon fishery became important. There are no reliable estimates of sport fish harvest before the sea lamprey invasion, and as recently as 1984 there were still no estimates of the lakewide sport fish harvest. However, creel surveys conducted by most management agencies have provided reliable estimates of the sport harvest for some portions of the lake.

The 1983 total lake trout angling catch estimated by all agencies except Michigan was about 100 000 kg and would probably be about 150 000 kg if Michigan catches were included (GLFC 1984).

Catches of exotic salmonids by anglers are also large and increasing. Catches of exotics, mainly rainbow trout, coho salmon (*Oncorhynchus kisutch*), and splake, in Wisconsin waters (including lake produced fish caught in tributary streams) have exceeded lake trout catches by about one third (Swanson 1981, 1982; Margenau 1983; Pratt 1984). Catches of exotics, mainly coho salmon, rainbow trout, and chinook salmon (*Oncorhynchus tshawytscha*), in Michigan and Minnesota are probably about half as large as catches of lake trout (J. Peck, Michigan Department of Natural Resources, and J. Spurrier, Minnesota Department of Natural Resources, pers. comm.). In Ontario waters the catches of exotics are much less than the catch of lake trout, but the exotics are gaining in importance as natural reproduction increases (Ontario does not stock exotics into Lake Superior).

Status of the Stocks

Inshore Lake Trout

Methods of assessment fishing and of data analysis for U.S. waters were described by Pycha and King (1975) and Pycha (1980). Canadian methods are similar, except that zone quotas were used for assessment whereas in U.S. waters, explicit assessment netting was conducted by or under the direction of state or federal agencies. For Canadian inshore zones since the early 1970s, lake trout caught incidentally in nets set for other species (mainly lake whitefish) were considered sufficient for assessment purposes. Management policy for the inshore zones was that there was no lake trout fishery as such, but that there was an acceptable incidental catch (the quota). As a result, no abundance estimates based on fishing directed at lake trout are available.

A variety of lake trout population changes that took place in different areas of Lake Superior after 1970 were related mainly to changes in stocking, fishing, or natural reproduction. Data on abundance of lake trout in U.S. waters were obtained from assessment fisheries conducted by the various states and were standardized, synthesized, and provided to us by R. L. Pycha (NFC-GL, pers. comm.). Changes in lake trout stocks in various inshore areas are illustrated in Fig. 2. To avoid redundancy, we discuss only the data for Wisconsin and central Michigan (Keweenaw Bay to Munising) which together adequately illustrate major trends.

The abundance of planted trout in Wisconsin was high in 1970–71 but declined sharply in 1972–73 and stabilized at a much lower level or slowly declined in 1976–81 (Fig. 2). This declining abundance of planted lake trout was associated with increased sport and commercial harvest and reduced planting.

The abundance of wild lake trout in Wisconsin increased in 1970–72, declined through 1977, increased in 1978–79, and

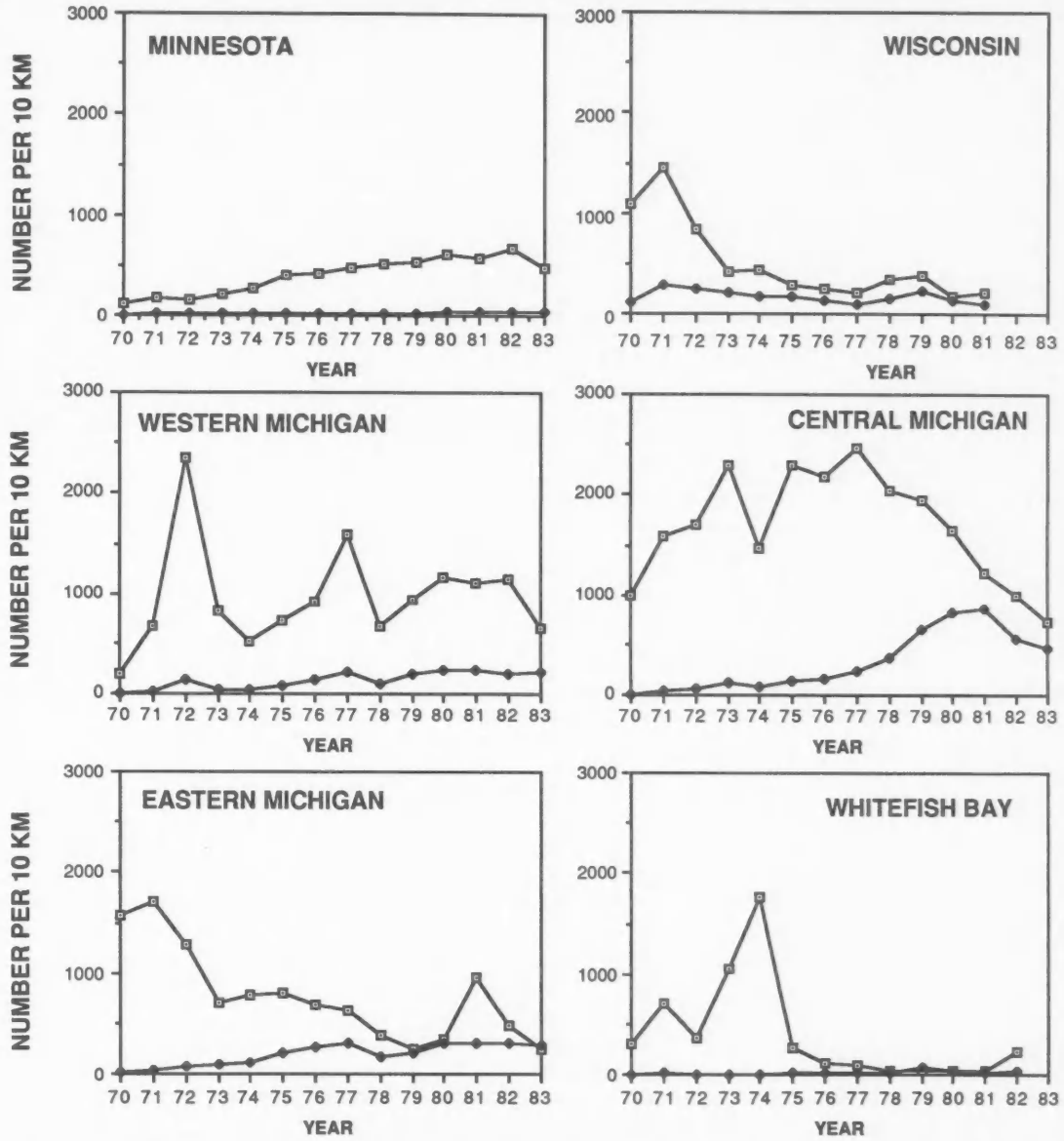

FIG. 2. Catch per unit of effort (CPUE) for planted lake trout (open squares) and wild lake trout (solid diamonds) in six areas of the U.S. waters of Lake Superior, 1970–83. Western Michigan is west of the Keweenaw Peninsula, central Michigan is east of the Keweenaw Peninsula to the vicinity of Marquette, and eastern Michigan is in the vicinity of and east of Munising.

declined sharply in 1980–81 (Fig. 2). High abundance of wild fish in 1970–72 was due to the recruitment of strong year-classes produced in the mid-1960s and declining abundance in 1973–77 was probably due to the production of weaker year-classes in the late 1960s and early 1970s, along with increased fishing. The increase in 1978–79 was probably caused by the recruitment of strong year-classes produced in about 1971–73. The decline in abundance in 1978–81 was probably the result of increased harvest.

In Wisconsin, most of the mainland shore is sand or clay and most of the historical lake trout reproduction was on offshore reefs. Reproduction of lake trout was documented as early as 1965 (GLFC 1966) and was mainly associated with a wild stock that spawned on the Gull – Michigan Island Reef (Swanson and Swedberg 1980), about 30 km offshore in eastern Wisconsin. Although evidence of limited natural reproduction has been found at numerous locations in Wisconsin (NFC-GL, unpubl. data), most wild fish were still produced on the Gull – Michigan Island Reef in the mid-1980s. Krueger et al. (1986), who examined the role of planted lake trout in Wisconsin, concluded

that little natural reproduction could be attributed to hatchery-reared fish. They reported that planted fish had largely failed to recolonize unoccupied historical spawning reefs, even though some of those reefs were only a few kilometres from the mainland shore. They also examined a stock – recruit relation at Sand Cut Reef, Wisconsin, and suggested that most of the changes in recruitment there were associated with changes in wild spawning stocks, even though planted fish were several times more abundant. They concluded that planted fish would have to be maintained at high abundance in Wisconsin to contribute significant reproduction, particularly on offshore reefs.

The abundance of planted lake trout in central Michigan, already high in 1970, increased to the highest level seen in U.S. waters in 1977, and then declined linearly in 1978–83 (Fig. 2). The increasing abundance in 1970–77 was associated with high stocking rates and the accumulation of fish of many ages (R. L. Pycha, pers. comm.). The decline in 1978–83 appeared to be a result of reduced stocking and of reduced growth rates that slowed recruitment into the sizes vulnerable to the assessment nets (R. L. Pycha, pers. comm.). The abundance of wild lake trout increased slowly from 1970 to 1974 and at an increasing rate in 1975–81 (Fig. 2), but then declined in 1981–83. The major increase in wild fish in 1977–81 and the decline in 1981–83 appeared to be strongly related to the pulse of wild fish in 1971–74; however, R. L. Pycha (pers. comm.) related the reproduction in the early 1970s to the planted fish then present. The reproduction of lake trout in central Michigan was documented in Keweenaw Bay as early as 1964, when 2-yr-old wild fish were first taken in trawls; others were taken each year from 1966 to 1972 (Swedberg 1985). Sampling with small-mesh gill nets in 1967–84 and with trawls in 1978–84 yielded juvenile wild lake trout at 18 of 19 locations sampled in central Michigan, and generally showed a trend toward increasing catch rates.

Lawrie (1978), who examined the lakewide relation between stocking rates and subsequent recruitment and abundance of stocked and wild fish in assessment and commercial fisheries, found a significant difference in the abundance of lake trout between two time periods, 1966–69 (47 fish/km of gill net) and 1970–76 (119 fish/km), chosen to provide a comparison between conditions before and after sea lamprey control. Fish caught in the earlier period were stocked before lamprey control became effective in 1961. He partitioned the improved catch per unit of effort (CPUE) in 1970–76 into 42.7 fish/km from increased planting, 18.1 fish/km from increased survival of planted trout, 0.7 fish/km from increased survival of native fish, and 10.5 fish/km from increased recruitment of native trout.

Offshore Lake Trout

Offshore lake trout can be separated into "lean" forms that inhabit offshore reefs or shoals, siscowets or "fats" that are often pelagic but also occupy deep waters, and "humpers" that occupy intermediate areas. Only the first two types are considered here. The offshore lake trout were generally somewhat affected by sea lamprey predation, but recovered much more rapidly than did inshore trout. Their faster recovery was almost certainly a result of two factors: they were subjected to less intensive lamprey predation, and abundance (especially of mature fish) never fell as low as it did in the inshore region. As early as 1966, GLFC

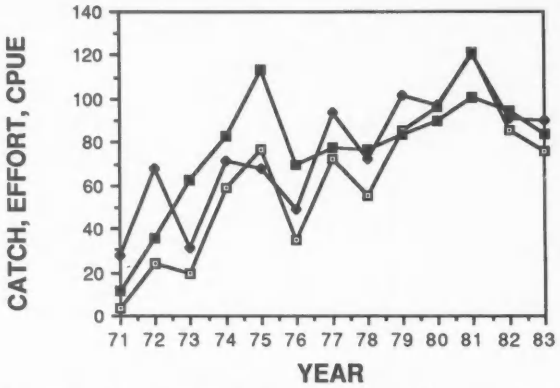

FIG. 3. Total commercial landings (thousands of kilograms, open squares), total gillnet effort (tens of kilometres, solid squares), and CPUE (kg/km, solid diamonds) of siscowets in U.S. waters of Lake Superior, 1971–83.

considered recommending a relaxation of fishing restrictions on a number of stocks, most of which were offshore (GLFC 1966).

Catches of siscowets were not separated from those of lean lake trout in the historical records. Siscowets are not now generally sought in Ontario waters because high concentrations of PCBs make their sale illegal. In Wisconsin and Michigan waters, a consistent and active fishery for siscowets is prosecuted with large-mesh gill nets (>114 mm) in deep water. During 1971–83, Wisconsin landings made up 71% of the lake's total harvest of siscowets (Fig. 3), and most of the rest were caught in Michigan. The commercial gillnet fishery directed at siscowets in Wisconsin and Michigan provides the best measure of abundance (Fig. 3). Catch, effort, and CPUE all increased substantially in 1971–81 and declined in 1982–83. Comparison of CPUEs in Wisconsin with those from the more limited fishing in Michigan (not shown here) indicated that siscowet abundance was nearly twice as high in Michigan as in Wisconsin. It is not known whether these levels of abundance are similar to those in pre-sea lamprey periods.

Stocks of lean lake trout occupy many offshore reefs or shoals and all are probably distinct. We discuss two areas, Michipicoten Island and Gull Island Reef, to illustrate major trends in offshore stocks.

For stocks of lean lake trout that inhabit the waters around Michipicoten Island, the 1984 fall CPUE was 255 kg/km, which is similar to the abundance estimates for a number of offshore grounds and well above the 65 kg/km (56.4 fish/km) reported by Lawrie (1978), who adjusted his estimates to account for the differences in efficiency between the net materials used in 1938–44 and modern nylon nets. The real difference in abundance is probably less than this because the 1984 estimate was based on fall fishing (CPUEs are usually higher in fall than during the rest of the year) whereas the 65 kg/km was probably based on a full-year fishery. Nonetheless, the abundance of lake trout around this island is probably at least equal to, if not higher than, that before the invasion of the sea lamprey.

Gull Island Reef, about 20–30 km from the mainland shore in eastern Wisconsin, is populated by lake trout indistinguishable from inshore lean forms. Catches of mature (prespawning, ripe, or spent) lake trout declined from 55 fish/km of gill net in 1952

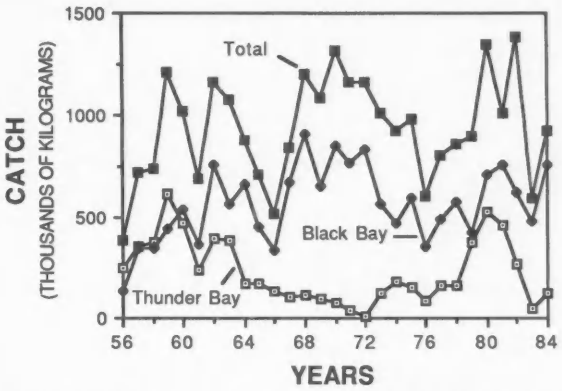

FIG. 4. Commercial catches of lake herring in Canadian waters of Lake Superior, 1956–84.

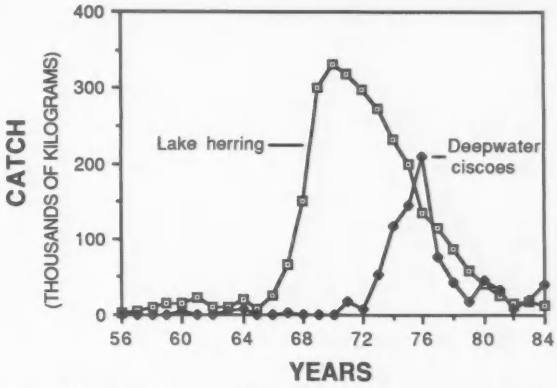

FIG. 5. Commercial catches of lake herring and deepwater ciscoes in eastern Lake Superior south of Cape Gargantua, 1956–84.

to less than 1 in 1960 and 1961 and then increased to over 200 fish by 1979 (Swanson and Swedberg 1980). Catches of mature males began to increase in 1962 and catches of mature females increased sharply in 1964. A second surge of mature fish in 1972–74 presumably resulted from the relatively strong year-classes produced 8–10 yr earlier. The recovery of lake trout on Gull Island Reef was consistent with a decline in sea lamprey wounding rate on fish longer than 600 mm from 33% in 1960 to 2.3% in 1963; thereafter, wounding rates fluctuated near the lower level (Swanson and Swedberg 1980).

Lake Herring

Ontario

Historically, most of Ontario's lake herring catch came from Thunder Bay and Black Bay. In the late 1950s, the catch in each bay was about 350 000 kg annually (Fig. 4). Harvests in Thunder Bay later declined from about 400 000 kg in 1962 to 7700 kg in 1972. A major cause of the reduced harvest was a decrease in fishing effort during the period, although limited information suggests that herring abundance was declining also. After the sea lamprey induced collapse of the lake trout and lake whitefish fisheries, the herring fishery alone was not sufficiently profitable to support a commercial operation, and many operators ceased fishing (G. Humby, Kemp Fishery, Thunder Bay, Ontario, pers. comm.). Catches averaged about 150 000 kg annually in 1973–78, increased dramatically to 538 000 kg in 1980, and then declined again as markets weakened. Trends in catch data suggest that the Thunder Bay herring stock would yield substantial catches if the fishery were profitable enough to prosecute.

Catches of herring in Black Bay remained relatively stable after the 1960s. Annual total catch quotas were introduced in Black Bay in 1972 because of concern about overfishing. The Black Bay fishery has produced about 400 000 to 730 000 kg annually from 1972 to 1986; most of the variation in catch can be attributed to differences in market conditions.

In Black Bay in the 1970s about two thirds of the annual catch were taken by trawls, in about 6 wk during the spawning season. A substantial portion of the catch was made up of spent fish. In the late 1970s, the market for herring eggs improved so sharply that the eggs became the most valuable part of the catch, and the fishing patterns shifted to take the herring before they spawned, to improve egg recovery. By the 1980s, most operators, including trawlers, converted to floating gill nets and fished earlier in the fall, so that virtually all quotas were filled before the fish spawned. The effects of this shift in technology have not yet been seen.

In eastern Lake Superior south of Cape Gargantua, annual catches of lake herring were less than 25 000 kg in 1956–66. The catch doubled in 1967, and doubled again in both 1968 and 1969; it peaked at 330 000 kg in 1970, and then declined steadily until 1983 (Fig. 5). The increase in the late 1960s was the result of increased activity of only a few commercial operators. The decline in the catch from 1971 to 1976 was caused by a shift in fishing pressure from lake herring to deepwater ciscoes, which were more profitable. During this period, both the mean size and the percentages of females in the catch increased. When the deepwater cisco markets declined in the late 1970s, operators who returned to herring fishing had a difficult time finding concentrations of the fish, and the herring catch continued to decrease.

United States

Lawrie and Rahrer (1972, 1973) described the growth and decline of the U.S. herring fishery and suggested that the decline was due to sequential overfishing of discrete stocks. From a maximum total harvest of over 8.6 million kg in 1941, the herring catch declined to 116 000 kg in 1981. A detailed analysis of the Wisconsin commercial fishery statistics from 1936 to 1970 (Selgeby 1982) showed that the fishery there was concentrated in six small areas and was restricted almost entirely to the spawning season. During the 35 yr of record, 55 million kg of herring were landed in Wisconsin, of which 48 million kg (87%) were taken from these six areas during the spawing season. Catches equalled or exceeded estimated levels of maximum sustainable yield in each of the six areas, and in each area the stock failed. Earlier herring declines in Minnesota and later ones in Michigan were probably the result of similar fishing patterns. After the major herring declines in U.S. waters, the fisheries persisted unrestricted until 1970 in Michigan and 1973 in Minnesota, when restrictions or bans were placed on certain fishing activities. No restrictions were imposed in Wisconsin. Lake herring catches generally declined in U. S. waters of Lake Superior in 1971–83 (Fig. 6), partly due to management actions and (especially after 1980) to weak markets. At times during the

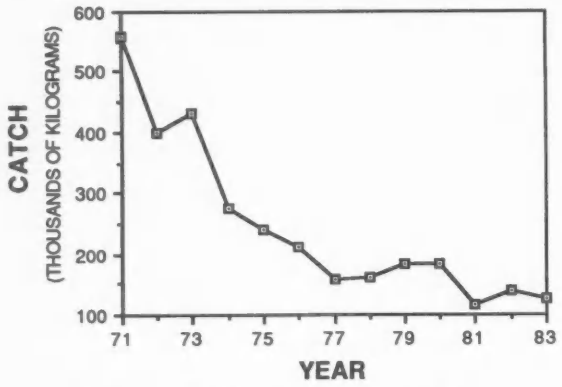

FIG. 6. Total commercial landings of lake herring in U. S. waters of Lake Superior, 1971–83.

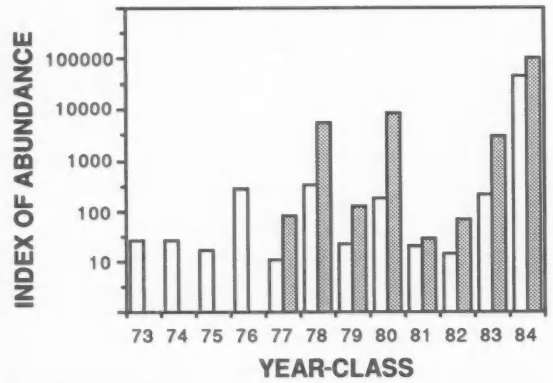

FIG. 7. Estimated year-class strength of lake herring in the Apostle Islands region of Lake Superior, 1973–84 (open bars), and in total U. S. waters of Lake Superior, 1977–84 (shaded bars).

1980s, fishing ceased in some areas because there was no market for herring.

After the major declines of lake herring, only relatively small populations persisted. Several hypotheses were offered to explain the failure of herring to rebound from the depressed levels; of these, the possibility of rainbow smelt predation on early life stages of herring has received the most attention. Selgeby et al. (1978) found evidence of relatively heavy smelt predation on herring larvae in Black Bay, Ontario. Although the herring stocks there have not been obviously affected by this predation, it seems possible that predation by a large smelt population on a small herring population in some other area might have effectively prevented herring from fully recovering.

After 1973 (possibly 1970 in the Duluth–Superior vicinity), herring year-class strength appeared to increase dramatically (Selgeby 1985). During assessment fishing in 1958–72, only one or two young-of-the-year or yearling herring were caught in any year (Selgeby 1985); in 1974, however, herring catches increased sharply. Strengths of herring year-classes were indexed from catches of yearlings in the Apostle Islands region of Wisconsin and along the entire U.S. shoreline (Fig. 7). During the periods of record, relative year-class strength varied from index levels of about 10 000 to 37 000 in the Apostle Islands

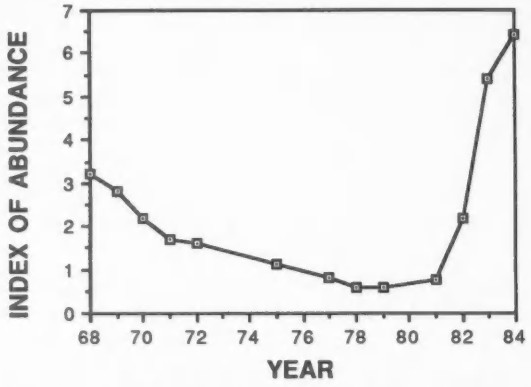

FIG. 8. Index of abundance of adult lake herring caught in gill nets (51- to 89-mm mesh, stretched measure) at many locations in U. S. waters of Lake Superior, 1968–84.

region and from 30 000 to 102 000 lakewide (U.S. waters). As year-classes accumulated in the near absence of fishing, catches of adult herring (>200 mm long) in assessment gill nets increased (Fig. 8). We anticipate that the immense 1984 year-class will result in a major upward surge in adult stocks as members of the year-class mature.

Although lake herring stocks in U.S. waters were apparently resurging and probably became more abundant than at any time in the past quarter century, the reason for that recovery was not obvious. The early phases coincided with a herring stocking program begun by the state of Minnesota in 1975, but relative strengths of year-classes appeared to be unrelated to the magnitude of the plantings. The recovery of herring also coincided with the implementation of various restrictions on the fisheries in Minnesota and Michigan. However, the relative degree of recovery appeared to be highest in Wisconsin, where no restrictions were enacted nor plantings made.

Despite the lack of restrictions in Wisconsin, landings of herring there declined 80% from 1970 to 1978 and remained low through 1984. The herring recovery was occurring despite the buildup of large populations of salmonid predators (previously discussed) and despite a near record abundance of rainbow smelt (discussed later) in 1976–78. Although the reason for the herring recovery is unclear, if the herring stocks in U.S. waters recover to their former abundance, they will be the first in the Great Lakes to do so after being depressed to such very low levels.

Lake Whitefish

Fisheries for lake whitefish are conducted in all jurisdictions except Minnesota, where catches are almost nil. Large-mesh gill nets (mostly 114 mm, extension measure) are used exclusively in Ontario and extensively in U.S. waters. Gill nets are fished throughout the year, even under the ice. Impounding gears (pound nets and trap nets) are also used during the open-water seasons in Wisconsin and Michigan. Lakewide catches of whitefish gradually increased from about 200 000 kg in 1960 to 800 000 kg in 1980 and then rose sharply to nearly 1 400 000 kg in 1984 (Fig. 9). Total catch trends were similar in Ontario and U.S. waters until 1973, but U.S. catches were generally two to three times as large as those in Ontario. After 1973, however, U.S. catches continued to increase while those

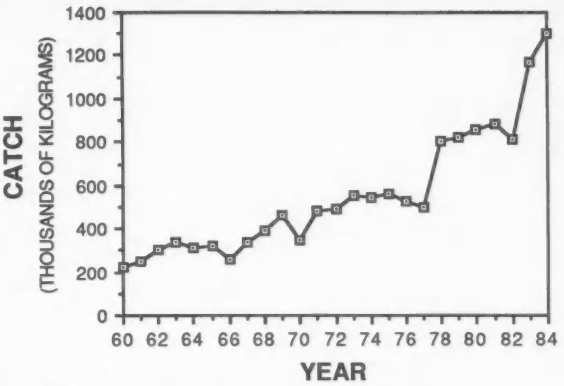

FIG. 9. Total commercial landings of lake whitefish from Lake Superior, 1960–84.

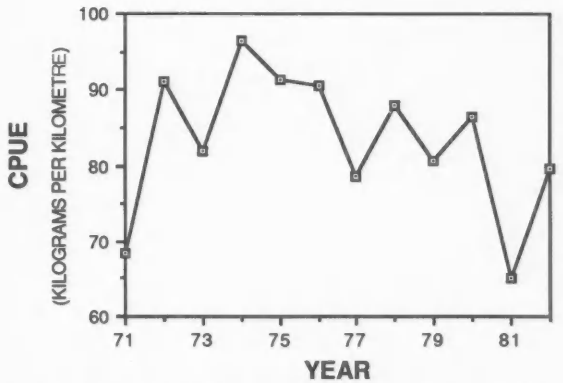

FIG. 10. CPUE (kg/lift) of lake whitefish in trap nets and pound nets in the U.S. waters of Lake Superior, 1971–82.

in Ontario stabilized, especially after catch quotas were allocated in eastern Ontario waters in 1977 and in the west in 1981. Total lake whitefish catches in 1975–84 substantially exceeded the long-term, pre-lamprey catches in Lake Superior, and the total catch in 1984 was the largest recorded since that in 1895. However, CPUEs from fisheries in U.S. waters showed that abundance declined somewhat after 1971 (Fig. 10) and that the very large catches in 1982–84 were taken from accumulated, previously unexploited stocks. Although lake whitefish catches increased progressively from 1960 to 1984, a number of stocks have been subjected to little or no exploitation. The evidence of the separateness of stocks (discussed below) comes from differences in population parameters. Three of these stocks are discussed here.

Western Michigan

In Michigan waters on the west side of the Keweenaw Peninsula, commercial production of lake whitefish probably began in the late 1800s. Records are lacking for the early years, but the fishery produced only about 21 000 kg annually in 1929–49. Catches declined sharply in 1957 and remained very low through the 1960s. In 1972, large-mesh gill nets were banned and whitefish catch was almost nil in 1973–82. In 1983, when an experimental trapnet fishery was begun to sample the whitefish stocks in the area, 780 trap net lifts yielded a total of 254 000 kg of whitefish (CPUE 326 kg/lift); in 1984, 1052 lifts yielded 262 000 kg (249 kg/lift). In the same years, the CPUEs for trapnet lifts in all other Michigan waters ranged from 27 to 66 kg/lift. In 1984 a new tribal fishery caught an additional 64 000 kg of lake whitefish in gill nets (Ebener et al. 1985). The average age and length of lake whitefish were 8.2 yr and 56.9 cm (n = 673) in the eastern half of this area and 7.2 yr and 58.7 cm (n = 126) in the western section (Ebener et al. 1985).

Lake whitefish along the west side of the Keweenaw Peninsula, under the protection of a closed fishery and sea lamprey control, had built up a large population that contained many large, old fish. Commercial harvests from this area were much larger in 1983–84 than in the pre-sea lamprey period.

Whitefish Bay

Commercial fishing is not permitted in the Canadian waters of the St. Mary's River. In 1978, the mean age of a total of 2000 whitefish sampled from Leigh's Bay in the river was 7.2 yr for males and 8.4 yr for females (66% of the females were 8 yr old or older). This age distribution contrasted sharply with that of a stock of whitefish that spawns at Gros Cap, about 1.5 km upstream and just outside the river mouth, which is subjected to a commercial fishery. The average age of Gros Cap fish was 5.4 yr for males and 5.6 yr for females; 5-yr-old fish at Gros Cap were the same size as 7-yr-old fish from Leigh's Bay.

In August 1984, when Fleischer and Ebener (1985) sampled commercial trapnet catches from a previously unfished location (about 9–10 km offshore) at the mouth of Whitefish Bay, a total of 615 whitefish included fish from 3 to 17 yr old. A catch curve analysis revealed that annual mortality (A) was only 0.38 for whitefish 6–17 yr old. Samples of whitefish catches from trap nets at more inshore locations in U.S. waters of Whitefish Bay in 1982–84 included few fish older than age 9, and annual total mortality of fish from ages 5 to 9 was 0.67 (Fleischer and Ebener 1985). Whitefish catches in U.S. waters of Whitefish Bay averaged 175 000 kg in 1978–82, about 1.75 times higher than the long-term (1929–49) U.S. commercial harvest from the bay. These examples are consistent with the assumption of multiple discrete stocks of lake whitefish, separated by only a few kilometres. The unexploited stocks at Leigh's Bay and offshore at the bay mouth contained much older and larger members than did the exploited stocks at Gros Cap and inshore Whitefish Bay.

Deepwater Ciscoes

Deepwater ciscoes are fished with small-mesh gill nets in the deeper waters of Lake Superior. Most of the U.S. catch is taken in Michigan and Wisconsin and most of the Canadian catch in eastern Lake Superior. During 1960–82, catches in U.S. waters were much larger than those in Canadian waters (Fig. 11) and catches in both jurisdictions were sharply declining in the 1980s.

We calculated estimates of catch, effort, and CPUE for U.S. waters for 1971–83 (Fig. 12), a period during which both catch and effort declined substantially. Clearly, the main cause for the decline in catch over the period was the decline in effort, although CPUE also declined in all jurisdictions. The CPUE for ciscoes in 1983 was 55% of that in 1971 in Minnesota, 79% in Wisconsin, and 83% in Michigan. Some evidence suggested that the abundance of deepwater ciscoes declined much more drastically than the CPUEs in the commercial fisheries suggest. Index netting (NFC-GL, unpubl. data) in Michigan waters

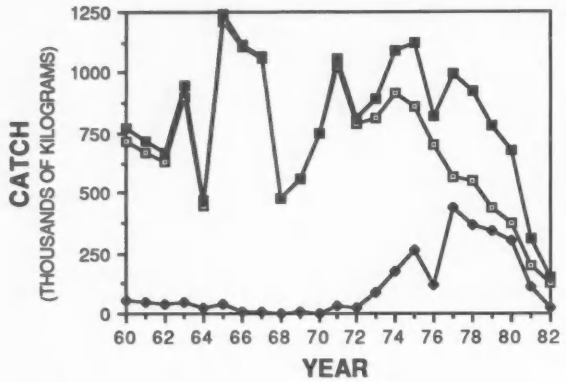

FIG. 11. Commercial landings of deepwater ciscoes (*Coregonus* sp.) in Lake Superior, 1960–82, from Canadian waters (solid diamonds), U.S. waters (open squares), and totals (solid squares).

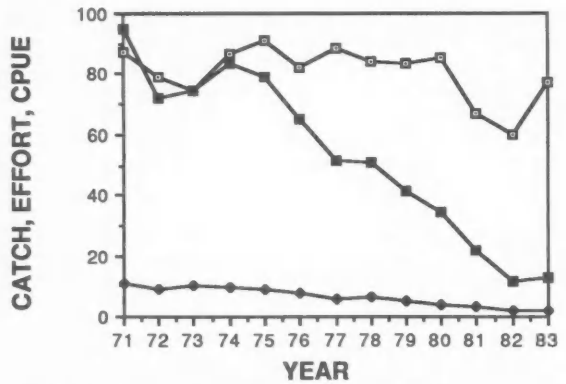

FIG. 12. Total commercial landings (ten thousands of kilograms, open squares), total gillnet effort (thousands of kilometres, solid squares), and CPUE (kg/km, solid diamonds) for deepwater ciscoes (*Coregonus* sp.) from U.S. waters of Lake Superior, 1971–83.

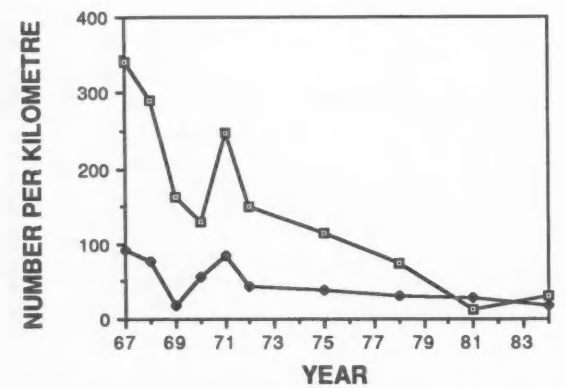

FIG. 13. Abundance (CPUE) of deepwater ciscoes (*Coregonus* sp.) in gill nets (51- to 89-mm, stretched measure) in the vicinity of the Keweenaw Peninsula (open squares) and Marquette, Michigan (solid diamonds), 1967–84.

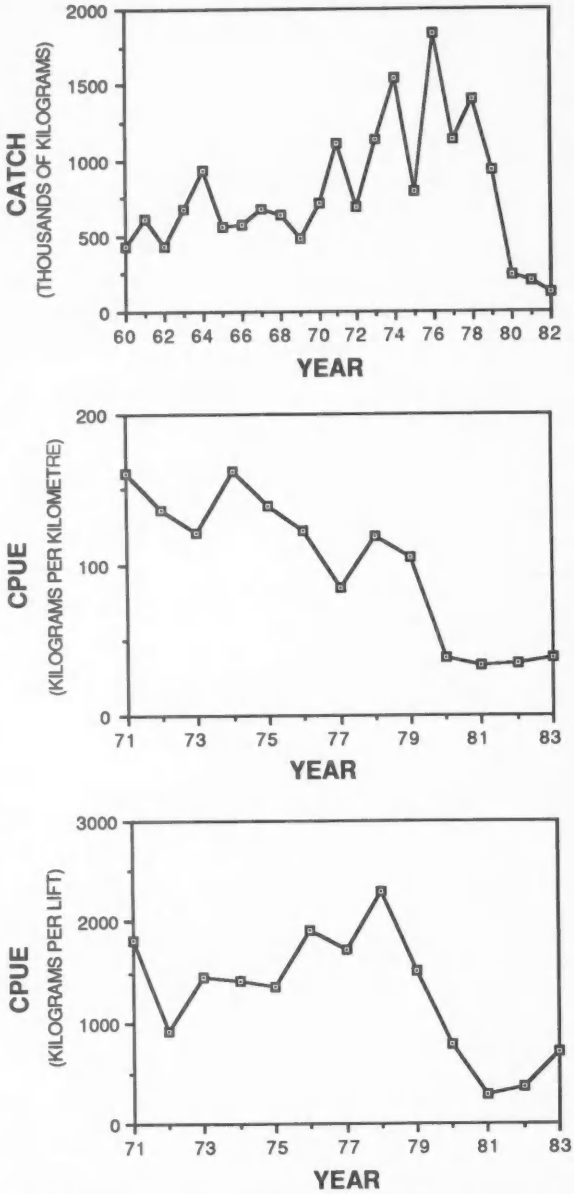

FIG. 14. Total commercial landings of rainbow smelt in Lake Superior, 1960–82 (upper panel), and abundance (CPUE) of rainbow smelt in 25- to 38-mm gill nets (center panel) and in pound nets (lower panel) in U.S. waters of Lake Superior, 1971–83.

somewhat shallower than those fished by the commercial fishery showed a 90% decline in CPUE during the period (Fig. 13).

Rainbow Smelt

Rainbow smelt are taken commercially in Lake Superior in small-mesh gill nets (primarily under ice bait fishing with suspended nets), trap nets, dipnets, and trawls. The pound net (U.S.) and dipnet (Ontario) fisheries are directed at spawning

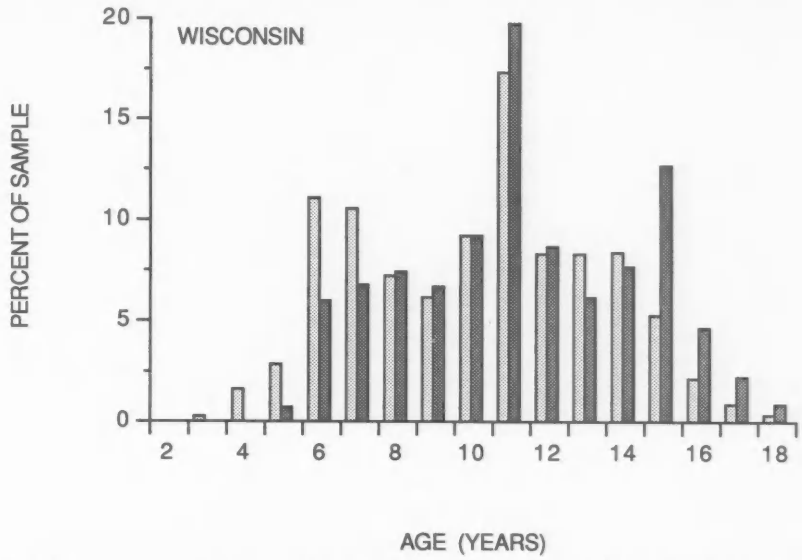

FIG. 15. Percentage contributions of various age-classes of walleyes (male, light bars; female, dark bars) to the 1981 spawning run in the St. Louis River.

aggregations. All significant commercial catches are taken in the western portion of the lake, from Thunder Bay, Ontario, to Ashland, Wisconsin. Large, but unmeasured catches are made by the recreational fishery with dipnets, seines, and lift nets, at many locations along the lake. In some years the sport catch probably equals or exceeds the commercial catch.

Commercial catches of rainbow smelt, which were relatively stable in 1960–70, increased to a maximum in 1976 and then declined sharply after 1978 (Fig. 14). Reduced catches after 1978 were associated with sharply declining abundance as measured by CPUE in several different types of gear (Fig. 14). However, CPUEs from the two fisheries during 1971–78 do not agree. The CPUEs from the gillnet fishery suggested declining abundance in 1971–78, whereas those from the poundnet fishery suggested a substantial increase in abundance during the same period. The gillnet fishery is much smaller than the poundnet fishery and takes only large smelt. Conversely, the poundnet fishery is directed at spawning aggregations, and is likely greatly affected by the duration and intensity of the spawning season, as well as by changes in abundance. Assessment catches in U.S. waters of Lake Superior more nearly reflect the trends in the poundnet fishery (Selgeby 1985).

Estimates of standing stocks of rainbow smelt in U.S. waters indicated that biomass may have declined more than 90% from 1978 to 1981, largely due to high mortality of fish older than 2 yr (Selgeby 1985). Catch data and observations of commercial, assessment, and sport catches in 1983 and 1984 indicate a considerable recent resurgence in abundance (NFC-GL, unpubl. data).

Walleyes

St. Louis River stock

Walleyes live in several suitable habitats in U.S. waters of Lake Superior; fish of the largest stock spawn in the St. Louis River, a major tributary that enters Lake Superior at Duluth, Minnesota (Fig. 1). The St. Louis walleye was probably fished heavily in the late 1800s and may have been adversely affected by pollution of the river with paper mill wastes as early as 1900. More recently, but before 1979, walleyes in the St. Louis River were only caught for fun by anglers because they were made almost inedible by the objectionable flavor of chlorophenolic products released from upstream paper mills (Margenau and Schram 1982). In fall, 1978, the Western Lake Superior Sanitary District began treating the domestic and industrial wastes from seven cities and 10 townships that included the paper mill wastes previously released into the St. Louis River. In the following spring a major fishery developed for walleyes when anglers discovered they were palatable, abundant, and large. The Minnesota and Wisconsin Departments of Natural Resources (DNR) then began studying this population.

The spawning walleyes sampled by the Wisconsin DNR in 1981 included many relatively old fish (Fig. 15); 60% of the males ($n = 677$) and 72% of the females ($n = 584$) were age 10 or older, and maximum ages were as great as 18 yr for males and 20 yr for females. Exceptionally old fish were also sampled by the Minnesota DNR in anglers' catches of walleyes in 1981 ($n = 491$) and 1982 ($n = 211$) (Fig. 16).

The size of the walleye spawning population was estimated to be 64 500 fish in 1981 on the basis of a mark–recapture study made by the Wisconsin DNR. As judged by estimates made by the Wisconsin and Minnesota DNRs, the total catches by anglers were 48 000 fish in 1980 and 22 000 in 1981. The creel surveys showed a much higher harvest in Minnesota than in Wisconsin and indicated that many of the fish caught in Minnesota were old and large whereas most of the harvest in Wisconsin was of juvenile fish.

Various Wisconsin DNR assessment studies revealed that much of this walleye population, especially the mature component, did not live in the St. Louis River or its estuary. The fish moved up the river from Lake Superior in early spring to spawn and returned to the lake shortly after spawning; there they ranged eastward along the shore (Margenau and Schram 1982).

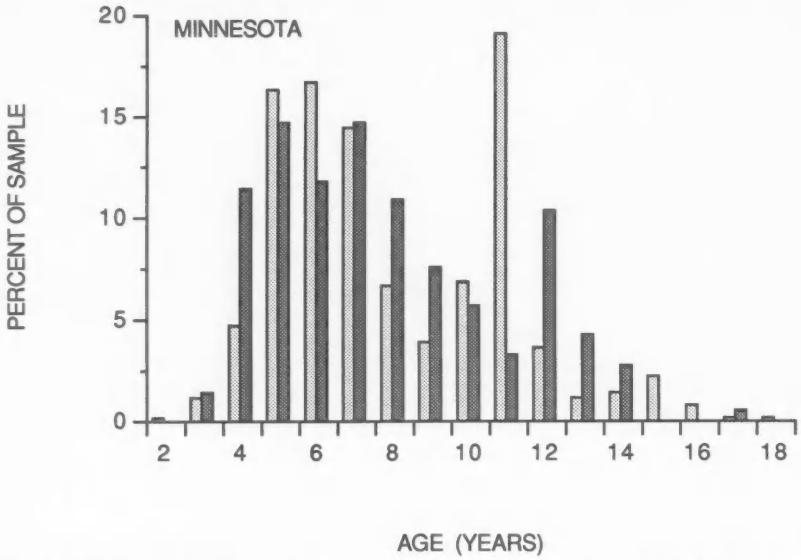

FIG. 16. Percentage contributions of various age-classes of walleyes caught by anglers in the St. Louis River in 981 (light bars) and 1982 (dark bars).

Most fish apparently moved along the Wisconsin shore toward the Apostle Islands but remained within about 60 km from the river. Some fish moved much farther, to the Apostle Islands area (about 80 km), and one fish was recaptured in Marquette Harbor, Michigan, about 400 km from the St. Louis River. This walleye population was once fished commercially in both Minnesota and Wisconsin. In the absence of commercial fishing and under extremely light angling pressure, the population built to a large size with many old members. The contrasts between the St. Louis River walleye population and populations in Black Bay and Nipigon Bay, Ontario (discussed next), are substantial.

Black Bay and Nipigon Bay stocks

No significant walleye stocks remain in Canadian Lake Superior. Commercial catches in Black Bay peaked at 170 000 kg in 1966 (Elsey 1972) and then dropped to 123 000, 52 000, and 9000 kg in successive years and finally to nil in 1972. The decline of this stock was attributed to overfishing (Colby and Nepszy 1981), and the stock has not recovered. In the final years of fishing, the catches included few or no mature fish. Factors that contributed to the increased pressure on this walleye population probably included the sea lamprey induced decline in lake trout and lake whitefish populations, and a fishery for saugers (*Stizostedion canadense*) that served as a vehicle for the marketing of "undersized walleyes." Walleyes that live in the tributary Black Sturgeon River have not expanded into Black Bay.

The only other substantial walleye stock in Canadian Lake Superior was in western Nipigon Bay. The decline and disappearance of that stock in the early 1960s was attributed by Ryder (1968) to local pulp mill effluent pollution downstream from the spawning grounds. However, the use of ultrasonic tags by Kelso (1977) showed that other species avoided the effluent plume, and Leslie and Kelso (1977) concluded that the pelagic larvae of other fish species that spawn in the river upstream from the pulp mill were not significantly affected by the plume. The apparent conflict implied in these findings can not be resolved here, but we suggest that overfishing may also have contributed to the loss of this stock.

Summary and Conclusions

The adverse effects of introductions (including invasions) and exploitation on the major native fish populations of Lake Superior have been, and continue to be, considerable, although many of the specific effects have not been measured. Within the past 25 yr, various management actions have resulted in the reduction of overexploitation, and in the control of sea lamprey populations. Intensive planting of lake trout and increasing natural reproduction have led to a resurgence in lake trout abundance; annual harvests in the commercial and recreational fishery are now about one third of the harvest formerly sustained. Lake herring, severely overexploited in almost all portions of the lake and perhaps also adversely affected by predation by sea lampreys and rainbow smelt, have recovered to their former abundance in Thunder Bay and appear to be in the log phase of a population recovery in U.S. waters. Lake whitefish have rebounded from depressed levels to the extent that the total commercial harvest in 1984 was the largest recorded in 90 yr, although such catches almost certainly cannot be sustained.

Deepwater ciscoes apparently increased in abundance as lake trout declined in the 1950s and 1960s and commercial catches increased greatly. Later the catches declined sharply, and probably abundance also declined. Although the CPUEs in commercial fisheries do not indicate a major reduction in cisco abundance, other evidence suggests that the stocks may be rapidly shrinking along the periphery of their depth range.

Rainbow smelt increased in abundance during a period when predators were scarce, and substantial commercial and sport fisheries developed for this species. In the late 1970s, however, the biomass of smelt declined sharply to only about 5–10% of its former level. Although the specific reason for this decline is

unclear, high mortality of adult smelt during the decline is consistent with other observations that indicate continuing heavy predation. In the early to mid-1980s, smelt abundance was again increasing.

The three major walleye stocks in Lake Superior showed dissimilar trends. Large walleye stocks in Black Bay and Nipigon Bay were eliminated by overfishing and perhaps pollution whereas a stock in the St. Louis River that was protected by its off flavor reached considerable size and included many unusually old fish.

In every species examined, recent trends indicate rapid changes. Various management actions to reduce exploitation and sea lamprey predation and to artificially enhance recruitment appear to be succeeding. Introductions of numerous exotic predators, most of which have established naturally reproducing populations, have increased the variety of predation possibilities and have stimulated angling. Contaminant levels do not appear to be adversely affecting populations of the major fishes, but have resulted in restrictions on the commercial sale of some lake trout.

Our overall impression is that most of the major native fish populations in Lake Superior are reverting toward their historic levels; however, the introduced species may be occupying some of the former habitat of native species and certainly are using some of the available forage. Although the outlook for the fish community of Lake Superior continues to improve, we stress that the current intensity of sea lamprey control and fishery management must be continued, or even increased to allow present trends to continue.

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Recent Changes in the Aquatic Food Web of Eastern Lake Ontario[1]

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During the past 10 yr there have been dramatic increases in piscivorous populations of walleye (*Stizostedion vitreum*) in the Bay of Quinte and of planted lake trout (*Salvelinus namaycush*) and double-crested cormorants (*Phalacrocorax auritus*) in the Kingston basin of Lake Ontario. This paper documents changes in the prey stocks shared by these piscivores, including reduction in size and abundance of the slimy sculpin (*Cottus cognatus*) with subsequent stock equilibration and unabated reduction in the size and abundance of rainbow smelt (*Osmerus mordax*), both owing to predation pressure from the lake trout. The third primary prey species, alewife (*Alosa pseudoharengus*), has not yet suffered severely from the depredations of the piscivores. Symptoms of the effects are discernible, however, and the implications of a possible collapse are discussed. Lake trout survival and growth have not yet been affected by the changes in prey availability, but their diet has shifted both in response to their own expanded size composition and relative abundance of the three prey species. Increased utilization of alewife makes the hunting of the trout more pelagic. Problems of obtaining representative samples of the prey are discussed.

Au cours des dix dernières années, on a observé un accroissement phénoménal des populations piscivores de doré jaune (*Stizostedion vitreum*) dans la baie de Quinte et de touladi (*Salvelinus namaycush*) ensemencé et de cormoran à aigrettes (*Phalacrocorax auritus*) dans le bassin de Kingston (lac Ontario). La présente étude documente les changements dans les stocks de proies partagés par ces deux poissons piscovores, y compris la diminution de la taille et de l'abondance du chabot visqueux (*Cottus cognatus*); cette diminution a été suivie d'un équilibre du stock et d'une baisse constante de la taille et de l'abondance de l'éperlan arc-en-ciel (*Osmerus mordax*). Ces deux événements sont le résultat de la pression par prédation exercée par le touladi. Le gaspareau (*Alosa pseudoharengus*), la troisième principale proie, n'a pas encore beaucoup été touché par la prédation exercée par les piscovores. On observe toutefois certaines incidences de cette prédation et on examine les conséquences d'un effondrement possible. Chez le touladi, la croissance et la survie n'ont pas encore été touchées par les variations de disponibilité de proies mais son régime alimentaire a changé en réaction à l'expansion de sa composition par taille et à l'abondance relative des trois espèces de proie. Étant donné que le touladi consomme plus de gaspareau, la recherche de cette proie s'effectue de plus en plus en milieu pélagique. On traite des problèmes de collecte d'échantillons représentatifs.

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The purpose of this paper is to assess recent changes in the fish community of the deep waters of the Kingston Basin of Lake Ontario in relation to the reintroduction of the lake trout (*Salvelinus namaycush*). Earlier studies (Christie 1972, 1973, 1974; Hurley and Christie 1977) chronicled the sequential collapses of many of the species populations which comprised the historical Lake Ontario fish community. The present work provides a description of the early stages of a recovery process which will take some years to complete.

The 1970 decade saw the institution of sea lamprey (*Petromyzon marinus*) control (Christie and Kolenosky 1980), improved control over commercial fishing effort via quota regulation, and the institution of intensive salmonid stocking programs. No less important, this was also the period of reduction of emissions of mercury, the chlorinated hydrocarbons DDT and PCB, and of municipally produced phosphates (Minns et al. 1986). The full effects of these initiatives on the biota of Lake Ontario are not yet clear, but it is possible to say that the changes to be described here have all been in the direction of return towards earlier system status.

The least equivocal response to management action has been the improved survival of stocked salmonids. After the collapse of the native stocks of lake trout and burbot (*Lota lota*), few

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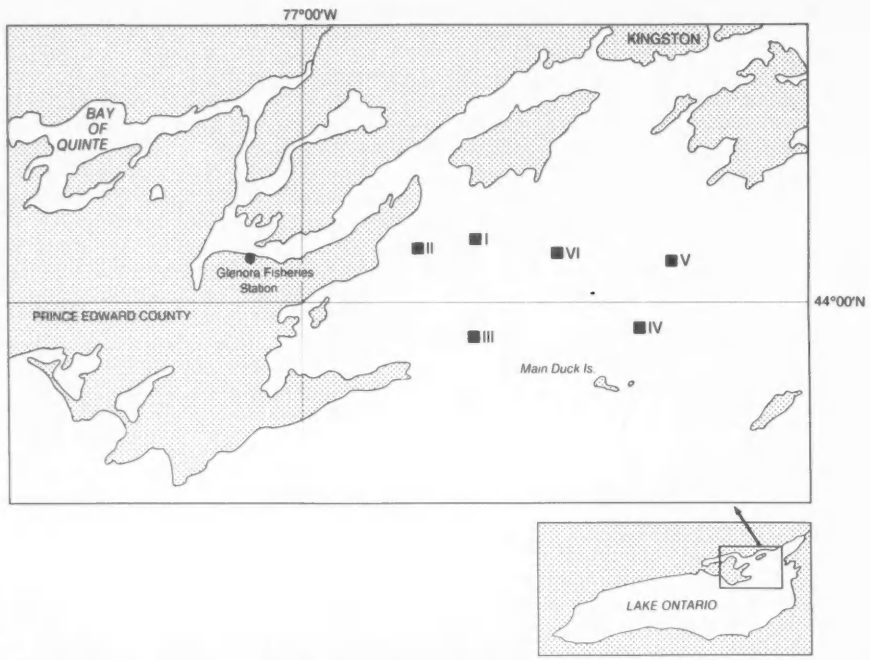

FIG. 1. Eastern Lake Ontario showing the Kingston basin and the Bay of Quinte. Index fishing stations are designated I–VI. They mark starting points for gillnet sets and trawl drags whose orientation varies with wind direction.

planted salmonids survived to reach maturity, and even the lake whitefish (*Coregonus clupeaformis*) stocks were heavily attacked by the sea lamprey (Christie and Kolenosky 1980). The control program for the lamprey was instituted in 1971, and since then stocks of lake trout, rainbow trout (*Salmo gairdneri*), brown trout (*S. trutta*), and the Pacific chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmons have all developed large populations. These successes have produced a new suite of management problems which includes concerns about the most suitable final species mix for the lake and about the levels of stocking intensity which might themselves be pathological for the system. These questions have no clear answers at present, but we offer the observations on lake trout – prey interactions below as a contribution to ongoing studies directed at both of them.

The long-term observation series on the Canadian side of Lake Ontario was focussed on the Kingston basin (Eastern Outlet Basin of Christie (1972, 1973)) because that area, with the contiguous Bay of Quinte, produced the largest historical fish yields of the entire lake and supported a number of important sport and commercial fisheries (Stone et al. 1954; Christie 1963, 1972; Hurley and Christie 1977). Its high productivity relates to the relatively shallow depths and to the fact that its islands and infolded shorelines constitute 72% of the entire lake perimeter (Christie 1973). It consists of an area of 376 km^2 separated from the main body of Lake Ontario to the southwest by a line of islands and shoals identified in recent literature as the Main Duck sill. The large Trent River drainage to the north enters the Kingston basin by way of the Bay of Quinte, and the basin is drained by the St. Lawrence River to the northeast (Fig. 1).

Eastern Lake Ontario offers several advantages for observing salmonid predator–prey effects. First, past research has been broadly based, and the series of annual observations on the fish community extends over many years. Second, the system is simple, in that the lake trout is believed to constitute the bulk of the salmonid biomass. Brown trout are stocked in the Kingston basin, but have not yet achieved high population densities. Rainbow trout are abundant in other areas of the lake, but there are no spawning populations in the Kingston basin tributaries, and the occasional captures are throught to be strays from the normal ranges of the stocks. This also applies to the pink salmon (*O. gorbuscha*) which has naturalized in the Great Lakes and is now seen in growing spawning runs in the streams of western Lake Ontario. The other two Pacific salmons are stocked only to the south and westward, and as with the rainbow trout, it is felt that any significant occurrence of pelagic fish in the relatively shallow Kingston basin would register in the bottom-oriented assessment nets. Captures of these fish are, however, extremely rare. Finally, the rest of the present community is comparatively simple as well. The rainbow smelt (*Osmerus mordax*), alewife (*Alosa pseudoharengus*), and slimy sculpin (*Cottus cognatus*) are the only broadly distributed species present in large numbers at or below the thermocline in the Kingston basin.

Methods

Six index fishing locations were selected in the Kingston basin of Lake Ontario (Fig. 1) in 1959, and with one exception (1965), they have been visited annually in summer ever since. Their choice was based on generally equal geographical spacing across the summer whitefish fishing grounds. The average

TABLE 1. Midsummer relative abundance estimates[a] for fishes sampled in the Kingston basin of Lake Ontario. Data from gillnet and trawl collections.

	Catch/gillnet lift (no.)					Catch/linear mi trawl drag (no.)		
Year	Alewife[b]	Smelt[b]	Lake herring	Lake whitefish	Lake trout	Slimy sculpin	Trout-perch	Johnny darter
1961	4.4	81.8		3.1	0.03			
1962	5.6	34.1		2.4	0.07			
1963	4.1	55.7	0.3	2.0	0.09			
1964	3.7	73.8	0.3	0.3	0.42			
1966	185.4	132.2	0.8	0.8	0.00			
1967	4.3	37.4	0.2	0.7	0.00			
1968	12.7	81.1	0.5	1.5	0.00			
1969	59.8	67.8	0.8	0.8	0.00			
1970	29.5	80.3	1.1	0.9	0.00			
1971	9.2	52.2	0.8	1.2	0.00			
1972	12.7	116.1	0.9	0.6	0.00	225.4	13.4	0.3
1973	5.5	67.9	0.7	0.5	0.00	460.3	25.7	1.0
1974	30.5	118.9	1.1	0.3	0.00	122.4	44.8	0.1
1975	8.4	140.9	1.1	0.8	0.88	137.0	27.1	0.7
1976	6.1	94.8	0.9	0.6	0.25	119.8	29.8	0.7
1977	0.2	84.3	0.7	0.6	0.92	106.8	19.1	1.6
1978	7.8	152.4	0.8	0.5	2.75	113.0	233.6	2.1
1979	7.8	147.1	0.8	0.4	3.08	138.9	196.7	2.0
1980	11.3	168.2	0.4	0.5	6.50	164.7	120.6	1.4
1981	24.8	114.1	1.3	1.8	3.00	149.8	86.4	3.0
1982	37.2	77.0	0.9	3.5	6.00	62.3	17.3	2.8
1983[c]	15.3	66.0	0.5	3.8	9.92	95.3	346.3	0.7
1984[d]	33.1	47.2	2.6	5.0	10.33	51.8	105.3	0.8
1985	10.7	46.4	1.0	3.0	17.50	112.3	87.7	4.0

[a]Six stations times three cruises averaged for June, July, and August. 100 yards each of 1.5- to 5-in. mesh in 0.5-in. intervals.

[b]Alewife and smelt data from bridled catches in 3-, 3.5-, 4-, and 2.5-, 3-, and 3.5-in. mesh sizes, respectively, with frequency as in footnote a.

[c]July and August cruises only.

[d]August cruise only.

depths of the index stations vary only between 26 and 29 m, reflecting the generally slight relief of the bottom in the area sampled.

Graded mesh gill nets have been used for sampling throughout the series and have been standardized since 1961. Specifications for all gillnet mesh sizes were developed to make the nets resemble those used in the commercial fishery in the late 1950's. The commercial whitefish nets (11.4-cm stretched measure) were hung slackly to produce a vertical diamond mesh which averaged 2.2 times longer than wide, and hanging specifications produced this configuration in all other mesh sizes. The commercial whitefish nets were usually 30 meshes deep. This produced a 3.1-m deep fence of netting in operation, and all mesh sizes in the assessment gear were hung to this specification. The twine was 210 denier/2 thread nylon for meshes up to 11.4 cm and 210/3 for 12.7 cm and larger meshes. Nets have been replaced on an approximately 3-yr rotation, and all mesh, net, and twine dimensions remained unchanged through the observation series (Table 1).

Mesh sizes are graduated in 1.3-cm intervals from 2.54- to 5.2-cm mesh. Nets are carried in metal boxes, or "trays," which contain 46 m each of the meshes 6.4–15.2 cm to a total of 366 m per tray. A linear "gang" consisted of the contents of four to six trays with the various mesh sizes distributed along its length. The three smallest mesh sizes were hung in 23-m lengths and one or two of the three nets units were fished per "gang" to reduce the large catches of small fish. Nets were set overnight, and typically each station was fished once per month from May through September.

Data on species growth, age, and relative abundance presented here have been averaged to approximate midsummer (July) values. With the exceptions of the alewife and smelt data discussed below, relative abundance (catch-per-unit-of-effort (CPE)) measured by the assessment gill nets is expressed as numbers caught per standard lift of 46 m each of the meshes 3.8–15.2 cm. There were departures from the seasonal schedule in various years, and where appropriate, the statistics in Table 1 were adjusted to compensate for missing monthly collections by use of average seasonal trends.

Gill nets may catch by gilling or entangling the fish in the netting, and smelt and alewife are only gilled in the two smallest gillnet mesh sizes. Thus, both the larger and smaller fish of both species are underrepresented in the collections. Both species are tangled in small numbers across the whole range of mesh sizes, however, and we have made use of these collections to extend the range of fish sizes analyzed.

More smelt than alewife are taken by tangling in the mesh sizes outside the gilling range. Their long teeth contribute to their capture and the process may not be based strictly on random encounter, in that the fish may actively "bait" to knots in the netting. There is an inverse correlation between the size of catch and the mesh size, and this means that capture probability

is some function of the amount of twine present to obstruct, or attract, a fish. Small smelt are always underrepresented in this sampling technique because they tend to fall free as the nets are lifted. This is true also for any fish whose size is small relative to the mesh size. The correlation between catch and total amount of twine was linear for size classes 15 cm (fork length) and greater in the 6.4, 7.6, and 8.9 meshes, and data from them were selected as most likely to be representative of the population at large.

These generalities apply to alewife as well except that the premaxillary bones and abdominal scutes contribute to their capture and it seems less likely that "baiting" contributes to their capture. Small alewife were less prone to be captured in this way and the data considered stable for calculation of relative abundance were those obtained from the 7.6, 8.9, and 10.2 mesh sizes.

Trawling did not become a regular part of the sampling routine until 1972. At that time the Ontario Ministry of Natural Resources adopted the use of the 3/4 "Yankee Standard" No. 35 net which was in use with the U.S. Fish and Wildlife Service, and it has been the gear used in all years since. It has a 12-m headrope with a 16-m sweep. Mesh size reduces from 9 cm at the mouth to 6.4 cm in the belly and 1.3 cm in the codend. The codend mesh was reduced by means of a 32-mm rochelle netting liner in 1977.

All trawls were made over a linear distance of 0.79 km measured from where full power is applied with the net on the bottom to where tow-power was reduced to retrieve the net. The towing speed varied around 4.7 km/h according to wind and current velocities.

Analytical procedures are described through the text and are largely conventional. One approach that may not be in routine use concerns the measures of condition applied to lake trout and alewife. In each case the method entailed computing annual logarithmic length–weight regressions from standard length ranges with equal numbers of samples used in each 10-mm cell.

The analytical procedure for trout stomach content data involved converting the length measurements of the fish identified from the stomachs to individual weights according to contemporary length–weight regressions and expressing the results as grams of prey per kilogram of trout. The number of fish that could not be identified was estimated and adjusted by the (seasonal) proportions for the identifiable fish, converted to weight values, and added to the species totals.

General Features of Change in the Vertebrate Biota of the Kingston Basin

The key features of historical change in the fish species composition of the Kingston basin through time have been documented (Christie 1972, 1973, 1974; Hurley 1986; Hurley and Christie 1977). This review illustrates more recent trends. The use of standardized sampling provides for relative abundance measures free of economic factors which biased the earlier commercial catch data and permits inclusion of species not taken by the commercial or recreational fisheries (Table 1).

The close biological linkage between the Bay of Quinte and the Kingston basin was discussed by Hurley and Christie (1977). Historically, large runs of whitefish and shallow water cisco or lake herring (*Coregonus artedii*) spawned in the bay and passed through the early life stages there. Alewife spawning runs to the bay were also very large and were thought especially important because of the predominant role of the alewife in the diet of the Bay of Quinte walleye (*Stizostedion vitreum*).

Adult walleye also made feeding migrations to the Kingston basin during the summers (Payne 1963), and the abrupt recovery of the stock to 1950's levels of density after the appearance of a very large 1978 year-class (Hurley 1986) has undoubtedly had significant impacts on the alewife of the open lake, as well as the Bay of Quinte.

The Bay of Quinte lake herring collapsed around 1945 and this coincided with the proliferation of smelt. Christie (1972, 1974) suggested that smelt may have been responsible for the declines observed in these coregonines both here and elsewhere in the Great Lakes. The Bay of Quinte whitefish stock failed to reproduce almost completely after 1955, and the walleye produced no significant year-classes between 1959 and 1978. Thus, during this period the alewife constituted the only known vector for materials flow from the lake into the Bay of Quinte.

By the mid-1960's, yellow perch (*Perca flavescens*) had replaced whitefish in the commercial fishery and the species subsequently produced yields up to 1 million kg/yr from the shoal waters of the Kingston basin. Yellow perch data from the six index stations were too irregular for inclusion in Table 1. Commercial fishermen believe, however, that the new fishery was enabled by a large increase in perch abundance.

The American eel (*Anguilla rostrata*) is another warmwater species of the Kingston basin which is not regularly taken in the assessment nets. The fishery for this species developed considerable importance in the mid-1960's as European demand increased. Annual yields doubled between the 1950 and 1970 decades, reaching a peak of 222 tonnes in 1978 (Kolenosky and Hendry 1982). There was evidence of growth overfishing (Pitcher and Hart 1982) according to Hurley and Christie (1982), but the commercial catch sampling observations offered no suggestion that the St. Lawrence Seaway construction, completed in 1958, impeded recruitment to the Lake Ontario stocks. In 1982 the fishery was closed because of high levels of contaminants in the fish, and it is presumed that this is currently resulting in increased biomass. This increased biomass may have major consequences for the biological economy of the Bay of Quinte and Kingston basin. These areas historically contributed 39 and 51%, respectively, to the annual catch of eels from Lake Ontario (Hurley 1973). By tracking concentrations of the chlorinated hydrocarbon Mirex (whose only known source is Lake Ontario), Dutil et al. (1985) showed that 74% of the eel yield taken in the St. Lawrence River to its debouchment on the Atlantic Ocean is of Lake Ontario origin, and thus the average yields from Lake Ontario during the period 1974–78, summed with the adjusted St. Lawrence values (Bourgeois et al. 1982), suggest that the total annual catch of Lake Ontario eels in this period was 761.5 tonnes/yr. There are no exploitation rate data with which to estimate standing stock, but given the length of the sedentary phase (Hurley 1972), it seems likely that this species represents a large component of the warmwater ichthyomass. The role of the eel in the food web is not well understood, but it is pertinent to the present discussion that before the collapse of the whitefish fishery in the early 1960's, they were known to descend to the depths of the commercial gill nets in late summer, where they ate tangled smelt and alewife, leaving characteristic knots of twine and fish bones in the nets. It seems likely that the eels were attracted to the dead fish because they have not been captured by trawling in the subsequent years of reduced summer gill netting intensity. This

does not rule out the possibility of active predation on these two species, however.

Lake whitefish have increased in relative abundance in recent years. These fish are members of the stock which spawns in Lake Ontario proper and which historically contributed 25% of the eastern Lake Ontario yields (Ihssen et al. 1981). Like the Bay of Quinte whitefish which spawns separately in the bay, this stock inhabits the Kingston basin in the summer. The primary diet item is the amphipod *Pontoporeia hoyi* (Ihssen et al. 1981). This organism is also the principal prey of the slimy sculpin (Brandt 1986), and this raises a question about how the use of the shared resource is partitioned between these species at equilibrium densities.

Since the collapse of the Bay of Quinte lake herring stocks, the small remaining population has been sustained by stocks which spawn in embayments along the south and western shores of the Prince Edward County peninsula (Fig. 1). The summer gillnet collections in the Kingston basin have been consistently small (Table 1), and without trend.

The other species taken regularly in the trawl sampling in addition to smelt, alewife, and slimy sculpin are the trout-perch (*Percopsis omiscomaycus*) and the johnny darter (*Etheostoma nigrum*). The latter species is taken with low frequency (Table 1). It will be noted that catches were approximately doubled by the use of smaller mesh in the trawl coderd after 1977, so it is unlikely that there have been any significant changes in population density.

However, the higher catches of trout-perch since 1978 probably represent a real abundance increase. This is because use of the smaller mesh during the first year (1977) showed no great change in the catch level and because in one recent year (1983), when the larger mesh was used again, the highest average CPE values were recorded. The recent density values are comparable with the values for slimy sculpin in the early years of the series. The distribution of the trout-perch is highly localized (it occurs mainly in the catches at station VI, Fig. 1), and this may account in some way for its general absence from the diet of the lake trout.

Waterfowl have always occupied an important place in the food webs of Lake Ontario, and some species have also changed greatly in abundance. The scaup (*Aythya marila*) has traditionally been the most numerous of the diving ducks and it visits the area in large numbers in spring and fall. Ross (1984) reported no major abundance changes, but he placed the average resource utilization in the Kingston basin at 1.7×10^6 duck-days during the fall migration and 1.9×10^6 during spring migration through the area. Their diet has not been studied extensively, but there is little question that the ducks extract large quantities of macrophytes and macrobenthos during their stay in the Kingston basin.

Piscivorous ducks of the genera *Mergus*, *Melanitta*, and *Clangula* are also numerous during migration. But the greatest known changes in abundance have occurred in the population of the double-crested cormorant (*Phalacrocorax auritus*). First, Price and Weseloh (1986) pointed out that the cormorant probably did not occur in Lake Ontario prior to the 1930 decade. Nest counts in the late 1930's suggested that a substantial population had been established and it increased greatly during the next decade. By the 1970's the population had dwindled to low levels, having been constrained by the levels of chlorinated hydrocarbons in the fish diet of the birds, and possibly also because of depredations by commercial fishermen (in the 1940's and early 1950's) who felt the cormorants competed with them for important fish, especially lake trout (Price and Weseloh 1986). These constraints were relaxed and by 1982 the eastern Lake Ontario population had grown from 22 pairs in 1974 to 770 nesting pairs (Price and Weseloh 1986). The population reached 2100 pairs in 1985 and remained unchanged in 1986 (D. V. Weseloh, Canadian Wildlife Service, Box 5050, Burlington, Ont. L7R 4A6, pers. comm.).

The ecological affects of these population increases are not known in detail, but there is little question about their significance. Acording to D. V. Weseloh (pers. comm.), the populations of 1985 and 1986 were in the order of 10 000 birds when nonbreeding individuals were taken into account. Given 6- to 7-mo feeding season, the large size of the birds (1.9 kg; Ross 1974), and a likely intake of fish between 20 and 30% of body weight per day (Dunn 1975), the consumption of fish in 1985 and 1986 was likely more than 800 tonnes and perhaps as much as 1200 tonnes. The cormorants confine their fishing to shallow water (mean depth 4.7 m, range 1.5–7.9 m; Ross 1974), and the species of fish represented in the diet reflect this in both freshwater and seawater. A sample of 38 nestling regurgitations was obtained at Pigeon Island, Lake Ontario, in early July 1985. The composite inclusions were 146 alewife, 1 rock bass (*Ambloplites rupestris*), 7 smallmouth bass (*Micropterus dolomieui*), and 3 yellow perch. Among the alewife, 54.5% were less than 100 mm fork length, suggesting that the cormorants were eating juveniles as well as spawning adults. Understanding of the extent of the impact of the birds on the alewife and other species will have to await the results of more extensive investigation of the cormorant food habits. Meanwhile, claims as to the effects of predation by lake trout and walleye on the alewife stocks should be tempered by the realization that bird predation on alewife could prove to be substantial. This is probably not the case with the other two prey species of the lake trout. The slimy sculpin and smelt live below the diving range of the cormorants (Godkin et al. 1982) and the migration of the smelt to the shoals for spawning largely predates the spring arrival of the cormorants (D. V. Weseloh, pers. comm.).

The ring-billed gull (*Larus delawarensis*) has also increased dramatically in abundance in recent years. Blokpoel and Tessier (1986) described population growth at the rate of 11%/yr to current levels where the four major island colonies of the eastern end of Lake Ontario support 150 000 breeding pairs. H. Blokpoel (Canadian Wildlife Service, Ottawa, Ont., K1A 0E7, pers. comm.) stated that the diet during the breeding period consists of smelt and alewife, but he has been unable to determine how much of the ration consists of live fish as opposed to fish found dead or dying during springtime mortalities of alewife in the nearshore zone (Graham 1956). The increased abundance of the gulls is also thought to be connected to the reductions in contaminant levels in the flesh of the fish they eat.

Changes in the Prey of the Lake Trout

Sculpin

The abundance of *C. cognatus* in Lake Ontario has been considered high for some time (Wells 1969). Godkin et al. (1982) discussed the high frequency of hybridization with its more shallowly distributed congener *Cottus bairdi* and suggest-

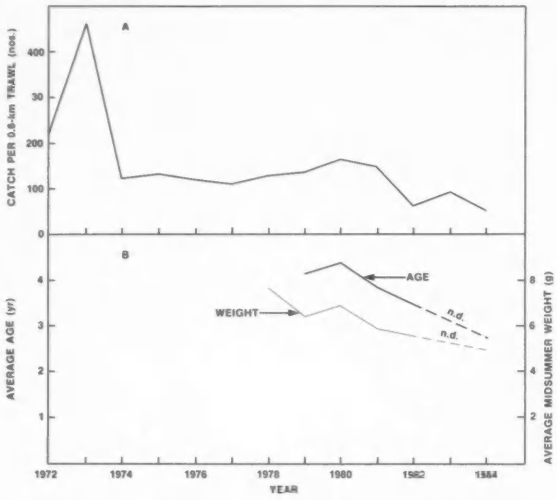

FIG. 2. Population trends for Kingston basin slimy sculpin. (A) Relative abundance from trawl catches. (B) Average age and weight changes. n.d. signifies no data collection (broken lines).

ed that the effect was at least in part a result of the high density of the slimy sculpin. The high abundance usually has been attributed to the loss of the piscivores lake trout and burbot (Christie 1973), but the reduction of abundance of the lake whitefish stocks after the early 1960's may also have helped the sculpin materially by way of decreased utilization of their shared food *P. hoyi*.

The high relative abundance of sculpin in 1972 and 1973 (Fig. 2A) predates the beginning of the trout biomass build-up, so the sharp decline in sculpin abundance after 1973 cannot be attributed to trout predation. The early collections (and that for 1983) were lost, so the abundance reduction cannot be evaluated in terms of age structure or other biological attributes. From 1974 onwards the numerical abundance was variable, with a slightly upward trend to 1981, followed by a decrease. The 1982–85 average was 38.9% lower than that for 1974–81. This abundance reduction was accompanied by a drop of 35% in the average age and of 34% in the average weight of the fish captured between 1979 and 1984 (Fig. 2B). The largest single reduction (27.9%) in sculpin biomass occurred after 1980. The inference is that the level of stock biomass was maintained through 1980 by increased compensatory recruitment in response to losses of older fish. Low recruitment, combined with the modest compensatory increase in growth rate indicated by the convergence of the size and age lines (Fig. 2B), was insufficient to sustain the biomass.

Smelt

Smelt first appeared in Lake Ontario in the late 1920's and proliferated in the years following World War II (Christie 1972). Spawning runs in Bay of Quinte streams were reported in the early stages of colonization, but subsequently, shore-spawning populations became more important in the eastern end of the lake. The commercial spawning run catches of eastern Lake Ontario were reduced from the first records of about 90 tonnes/yr in 1952 and 1953 to about one-half that level by the mid-1960's. There followed a resurgence to about the 90 tonnes/yr level in the early 1970's and then another irregular decline to a plateau in the 20–35 tonnes/yr range during the 1980's (Baldwin et al. 1979). Their catch variations prior to the mid-1970's largely reflected harvest and market conditions. The recreational harvest has not been measured, but local observation suggested that it was small relative to the commercial harvest and that there were only minor variations in the sport fishing effort until about 1983 when the fishing success had fallen to unattractive levels.

The relative abundance of smelt increased (Fig. 3A) between 1960 and 1976, at the same time that commercial fishing effort declined. Midsummer estimates of CPE at age were used to calculate survival as

$$(1)\quad S = \frac{Q_{j+1} + \ldots + Q_{j+(n+1)}}{Q_j + \ldots + Q_{j+(n)}}$$

where S = between-years survival rate, Q = experimental gillnet catch per lift, j = age at first capture (3 in this case), and n = year. These values were converted to measures of the between-years instantaneous total mortality rate (Ricker 1975), which were averaged arithmetically to approximate within-season values representing age 4 and older fish. This approximates the range of sizes of smelt taken by the commercial gill nets.

Ten pairs of effort and mortality values between 1959 and 1971 were compared (the missing 1965 observations cost 3 yr from this series). The correlation is highly significant ($r = 0.70$, $P < 0.01$) and the linear regression equation is

$$(2)\quad \hat{Z} = 0.2483 + 0.001322f$$

where $\hat{Z}$ = instantaneous rate of total mortality and f = reported effort in 1000-m gillnet units.

The reason the series was truncated at 1971 is that a general shift in catchability occurred at that time. Relative abundance indices from the experimental gill netting (Table 1) for both the early and later periods were highly correlated with the spring commercial CPE estimates when only age 4 and older fish were included in the analysis. After 1971, the slope of the regression was 2.3 times lower, and the variance in the relationship increased. There was no major change in the gill nets used. A large proportion of the total catch in this fishery was taken by a small number of fishermen, and it has been suggested (by fishermen) that the retirement of a single major operator in 1971, and the addition of several younger but less experienced fishermen whose fishing included more time outside the period of peak spawning run concentration of the smelt, was sufficient to the bring about this reduction in fleet efficiency. Even when this change in catchability is statistically adjusted by the factor 2.3, however, the fishing effort shows no increase through the latter years of the 1970 decade and the first half of the 1980's when smelt abundance returned to levels as low as those seen in the years of intensive commercial fishing early in the series.

The reduction in numerical density of the smelt after 1980 is consistent with the hypothesis that they were reduced by lake trout predation. Note first that the abundance of age 3 smelt generally paralleled that for smelt of all ages (Fig. 3A) in the years up to 1977, and this reflects the strong representation of older fish in the stock sampled. For the years 1961–76, age 2 fish contributed 20.7% of the total CPE for all fish older than 2 (yearling fish averaged only 3.6% of the total for all ages). From 1977 through 1984, age 2 fish contributed 46.3% of the age 2 and older CPE, while the four observations between 1978 and 1981 alone reached 56.6%. After 1977 the stock of older fish

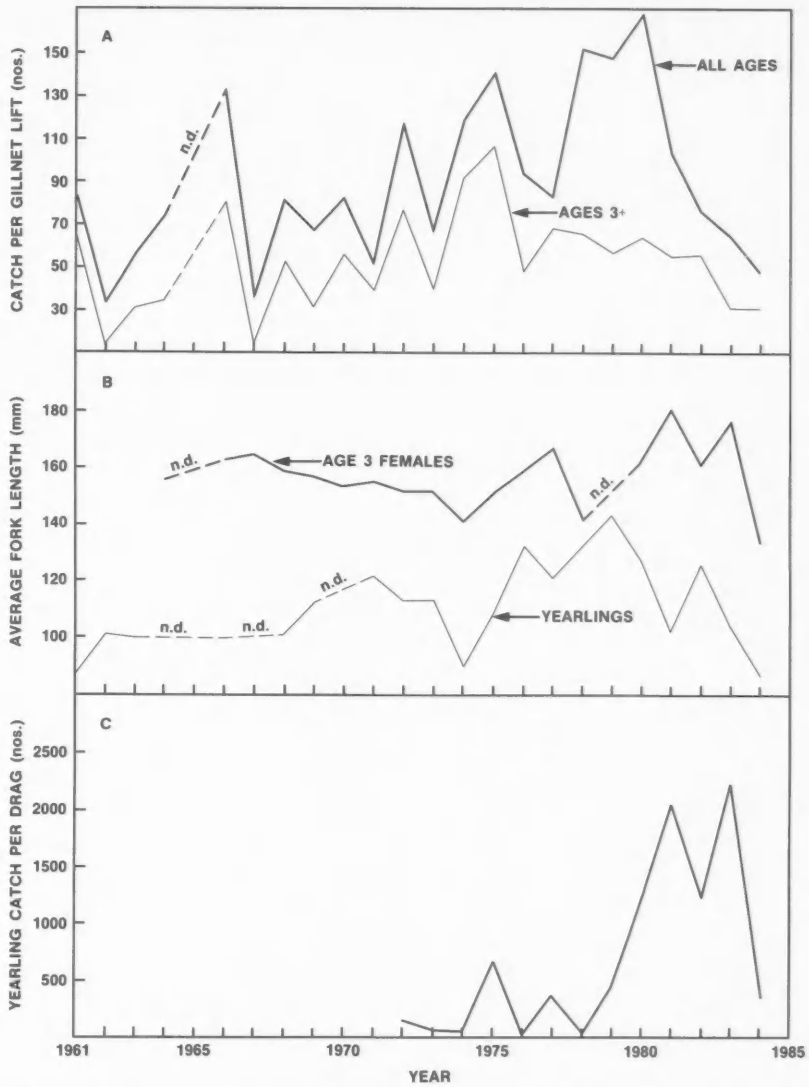

FIG. 3. Population trends for Kingston basin smelt. (A) Relative abundance from gillnet catches (see text) for fish of all ages (solid lines) and fish ages 3 and older (broken line). (B) Average midsummer lengths for age 3 females and yearlings. (C) Relative abundance of yearlings based on trawl catches. n.d. signifies no data collection (broken lines).

declined slowly at first, and then precipitously, improved recruitment of 2-yr-olds allowed the numerical increase to continue to 1980 after which the decline was general. The numbers of yearling fish taken in the bottom trawls increased strongly, beginning with 1979 year-class fish in 1980 and continuing through the recruitment of 1982 year-class fish in 1985 (Fig. 3C). It appears, therefore, that the surge of age 2 fish recruited to the gill nets through 1978, 1979, and 1980 did not come from strong year-classes available to the trawls. The simplest explanation for this unusual sequence is that young fish were normally pelagic, and as larger fish were cropped down by the lake trout near the bottom, progressively smaller fish occupied the benthic habitat. This suggestion is consistent with the observations reviewed by Evans and Loftus (1987), and as they point out, the mechanism for separation of young and adults when both are present could be either competitive exclusion or cannibalism.

This likely shifting in the spatial distributions of the size- and/or age-classes complicates interpretation of both mortality and size-at-age data. The general rise in average size of the yearlings between 1974 and 1979 (Fig. 3B) coincides in a general way with a reduction in alewife density from the 1974 peak. It is also consistent with the smelt abundance variations, however, in that when older smelt were abundant on the bottom,

the smaller yearlings were more likely to be eliminated, or otherwise excluded. There can thus be no fully convincing case made for either inter- or intraspecific competition effects on the growth of smelt yearlings.

The case for density dependence in the growth of older smelt is somewhat more convincing. As an example, the length of age 3 females moved gently downwards through the period 1966–74, while the population of older fish was increasing, and with some variation, it increased after these fish became less abundant. The trends are somewhat less clear after 1974 because year-to-year variance increased, but it is noteworthy that size of fish of all ages was significantly reduced in the most recent observations. This will bear close scrutiny in the ongoing sampling because it is best explained in terms of size-selective mortality.

Alewife

The population biology of the alewife in Lake Ontario is poorly understood. The Kingston basin sampling takes place while large spawning runs of alewife ascend the Bay of Quinte from Lake Ontario. The relative abundance trends for the two areas show some paralleling (Table 1, and see also Hurley and Christie 1977), and while the correlation is weak (P falls just below 0.05 at 20 df), it is suggestive that the stocks share causal mechanisms for their dynamic properties or that the causal mechanisms are correlated.

The alewife sampled in both areas are subject to great year-to-year variations in numerical abundance, but while gillnet CPE varied 30-fold in the Bay of Quinte through the period 1961–84, the Kingston basin values varied 200-fold in the same time period (Fig. 4). There is a large random error component in both data sets which is probably associated with the schooling behaviour of the fish. The CPE values for the companion trawl and gillnet assessments since 1972 in the Kingston basin are highly correlated ($P < 0.01$), however, and this indicates that the high variance is at least not strictly related to the peculiar characteristics of the gill nets (i.e. overnight sets, tangling) and may have a more complex basis than that observed in the Bay of Quinte.

One possible explanation for this difference lies with the winter and spring mortalities that are frequently observed with this species (Graham 1956). In springs when the shores of the open lake are littered with dead and dying alewife, no such mortalities are observed within the Bay of Quinte. The inference from the work of Graham (1956) in the area is that the bay runs consist of temperature-acclimated survivors. An equally viable and not incompatible explanation concerns distributional variance. The areas of the bay sampled during the alewife spawning runs are homothermous and warm, while the 15°C isotherm, which is thought to represent the preferred temperature of alewife (Otto et al. 1976), only approaches the sampled bottom areas of the Kingston basin in exceptionally warm years and during seiche action. The catchability variations may therefore be climatically induced, and the issue deserves study. Meanwhile, we are satisfied that the generally declining abundance trends between 1966 and 1977 and the abundance recovery after 1977 are representative (Fig. 4A), but we place less than full confidence in the year-to-year particulars.

The 1966, 1969, and 1974 peaks were progressively lower, and running averages through the data (Fig. 4A) show a distinct downtrend to the point of collapse in 1977. This trend was paralleled by declines in mean age, condition, and the growth of age 2 fish. This has several important implications.

First, the mortality of the winter of 1976–77 was likely weather related, as O'Gorman et al. (1987) suggest, but these data indicate that growth, condition, and recruitment had been declining in the stock for some time, likely predisposing it to collapse.

As O'Gorman et al. (1987) found, the correlation between fish condition and relative abundance in the 1978–84 period (Fig. 4A, 4B) was negative, and significant ($r = -0.82$, $0.05 > P > 0.01$), suggesting an intraspecific competition effect. For the earlier years of the series, however, there is a weak ($r = 0.38$) but positive correlation between alewife condition and relative abundance. One possible explanation is that the increased availability of juvenile smelt on the bottom (Fig. 3C) reflected an overall increase in numerical abundance rather than a simple shift in vertical distribution. If so, the decline in alewife condition could have resulted from inter- as well as intraspecific competition. This is consistent with the diet overlap between young smelt and the alewives discussed by O'Gorman et al. (1987). It also suggests a mechanism which allowed for high condition values in the alewife in the early years, when their densities exceeded recently observed levels. Rising smelt abundance through the 1967–78 period in particular could have produced the downward trend in alewife abundance by either predation on juveniles (Evans and Loftus 1987) or competition for planktonic food, and the reduced alewife condition could have been attributable to the competitive interaction.

As already noted, the best available explanation for the increase in smelt abundance lies with the improved survival associated with reduced fishing pressure. The reciprocal trends for alewife and smelt abundance may not have been causally related, but if there was interaction, we argue that it operated through impact of smelt upon alewife, rather than the reverse.

Mean age (Fig. 4C) is not a very sensitive statistic because of the difficulties discussed by O'Gorman et al. in identifying the crowded annuli on the scales of fish older than about three winters. The range of variation of 1.5 yr (Fig. 4C) is thus narrower than in reality and is most strongly influenced by the relative contributions of the young fish. The analysis of the scales has also not kept abreast of data collections, leaving serious gaps in the record.

In years of high alewife CPE, the sample collections typically revealed higher average age and the reverse (Fig. 4A, 4C). For the years 1961–79, the correlation was significant ($r = 0.57$ for 12 df, $P < 0.05$) and it yielded the linear equation

$$(3) \quad \hat{A} = 2.181 + 0.019\ \mathrm{CPE}$$

where $\hat{A}$ = predicted average age in years and CPE = catch per gillnet lift (see Methods). The addition of the four data pairs for 1980–83 yielded a nonsignificant correlation coefficient and reduced the amount of variance in average age accounted for by abundance from 32.5 to 16.8%. The data are not conclusive, but they suggest that the decline in mean age from 1980 onwards represented the first evidence of the impact of piscivory on the alewife stocks (Fig. 4C).

Dynamics of the Lake Trout Stock

Survival and Growth

The native lake trout stocks of Lake Ontario declined continuously through the 1930's and 1940's, and by the early 1950's they were too sparse to be of interest to fishermen (Christie 1972). Trial plantings were undertaken cooperatively

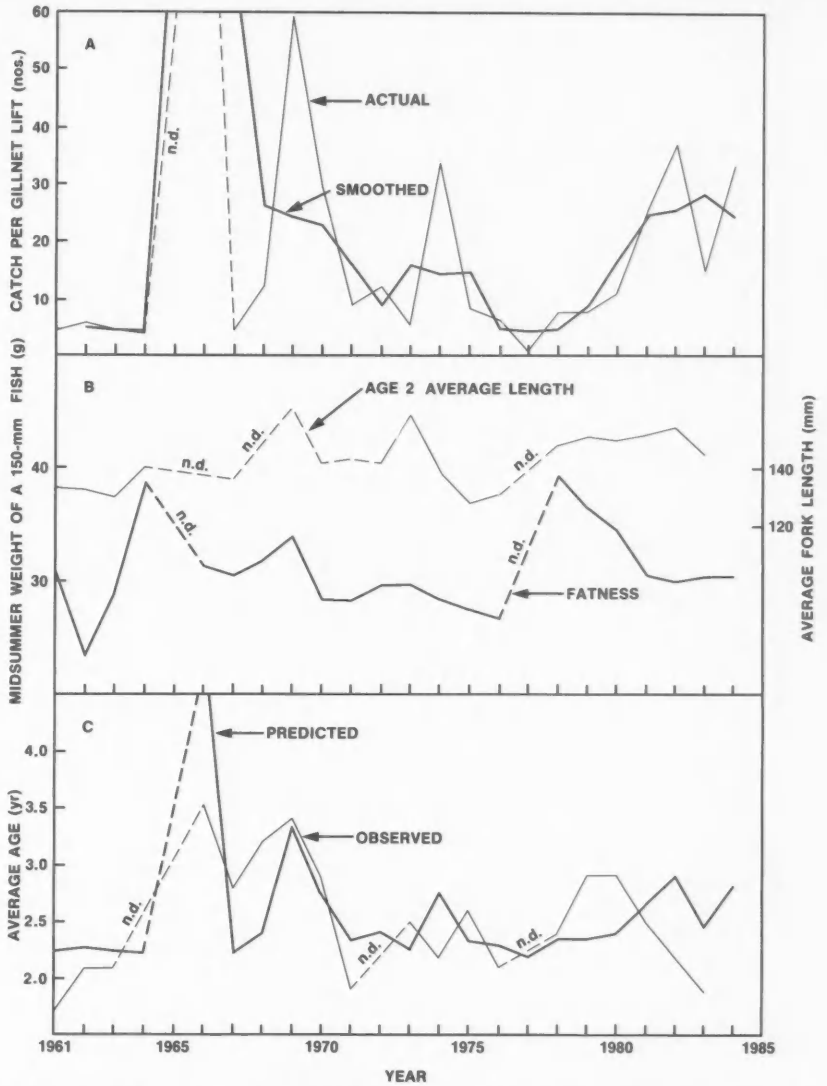

FIG. 4. Population trends for Kingston basin alewife. (A) Relative abundance from gillnet catches (see text) as observed (solid line) and with data smoothed by threes (broken line). (B) Growth of age 2 fish (broken line) and condition as weight of a 150-mm fish (solid line). (C) Average age as observed (solid line) and as predicted from relative abundance (broken line, see text). n.d. signifies no data collection (broken lines).

by the state of New York and the province of Ontario between 1954 and 1964. The plantings ranged between 10 000 and 40 000 fin-clipped yearling fish and increased to 60 000 and 100 000 yearlings in 1963 and 1964. Examination of a sample of 5298 lake trout taken as by-catch in the operations of the commercial whitefish fishery between 1955 and 1961 contained just under 1% unmarked fish, a value readily explained on the basis of error associated with the marking process in the hatchery. This confirmed that the native fish were extinct, or nearly so, by that time. Further results of the experiments were that few of the planted fish survived to reach sexual maturity (age 5 in females) and that mortality was correlated with the frequency of wounds caused by sea lamprey attacks on the trout (Christie 1974). The planting produced little accumulation of lake trout, and the low catches in the assessment gill nets through the 1960's and early 1970's reflect this (Table 1).

By contrast, the large recent CPE's in the Kingston basin show substantial accumulation of planted fish, and this relates to both improved trout survival and the large numbers of fish stocked. The lake trout reintroduction programs of the Ontario Ministry of Natural Resources and the New York Department of Environmental Conservation were started in 1973 and intensi-

TABLE 2. Numbers of yearling lake trout planted in Lake Ontario, 1973–84.

	Ontario[a]		New York[b]		
Year	East	West	East	West	Total
1973			66 000		66 000
1974			127 000		127 000
1975[c]					
1976	100 000	94 120	57 235	5 685	257 040
1977	200 900	87 600			288 500
1978	100 000	100 000	128 335	376 875	705 210
1979	100 000	101 416	156 200	336 205	693 821
1980	198 580	184 516	296 467	715 594	1 395 157
1981	200 380	186 932	343 300	687 800	1 418 412
1982	200 043	191 155	344 950	708 970	1 445 118
1983	186 900	184 700	370 800	715 500	1 457 900
1984	327 925	165 188	270 325	774 700	1 538 136

[a]All eastern plantings between Main Duck Island Charity Shoal in the Kingston basin.

[b]New York east includes plantings at Stony Island and Dablon Point, in the Kingston basin. New York west includes plantings at Selkirk, Sodus, Hamlin, and Niagara.

[c]No yearling plantings.

fied in the following years. The plantings have usually involved 1-yr-old fish released in the spring of each year (Table 2). The fish used have come from a variety of brood stock sources, but for present purposes the lake trout are dealt with as an homogenous population.

Spawning aggregations of trout are currently observed at a number of sites, and they contain a broad range of fish sizes and ages (Sly and Schneider 1984). The fin clips used on the stocked fish indicate that there has been no significant natural recruitment into the population as yet.

The recent rise in relative abundance of the trout in the Kingston basin has been continuous since 1977 (Table 1), suggesting that density of the introduced fish has not yet begun to influence their survival. The correlation between the July catch per standard gillnet lift (see Methods) of fish previously stocked by Ontario and the cumulative total Canadian number planted in the Kingston basin up to the relevant census year is linear (Fig. 5). The points for the two years 1981 and 1982 occupy anomalous positions in the graph, but given the return of the 1983 and 1984 data points to appropriate positions in the linear array, it is taken that the outliers were caused by low catchability in both years and that, with a lag of 2 yr, 100 000 fish stocked yields 9.8 more fish per unit of effort on average.

Analysis of biomass change also supported the hypothesis that lake trout density had not become self-limiting through the study period. The average growth rate shown in Fig. 6 is faster than that observed in the earlier series (1961–64), where size-selective cropping by the lamprey was responsible for the lower size-for-age values measured. Note also that the growth was similar for trout taken in a recent companion observation series in western Lake Ontario, where other large stocks of piscivorous salmonids as well as the lake trout utilize a comparable base of prey species.

The average lengths for the various ages of trout varied within narrow limits through time and revealed no significant trend. Similarly, the average length–weight relationship for the lake trout described by

$$(4) \quad \log W = 3.21/\log L - 5.422,$$

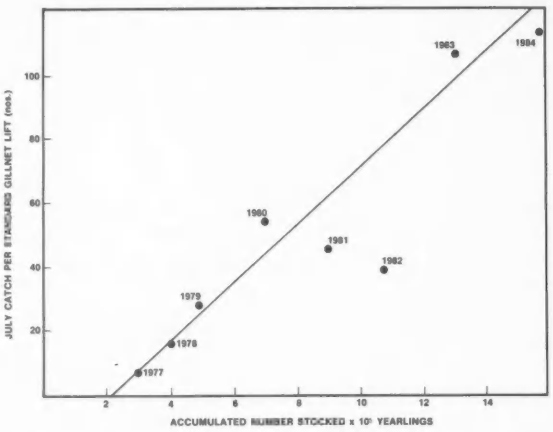

FIG. 5. Relative abundance of lake trout from summer assessment in the Kingston basin in relation to numbers stocked, both referrable to Canadian stocked fish only.

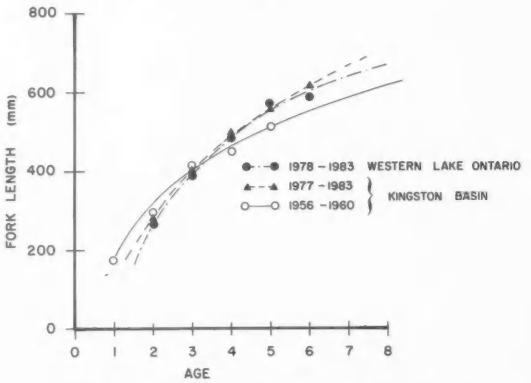

FIG. 6. Growth of planted lake trout in Lake Ontario.

where W = is the estimated weight (grams) and L = length (millimetres), varied somewhat from year to year under presumably exogenous influences, but there was no trend evinced which could be statistically linked to growth rate or fish density.

The biomass of small lake trout did not accumulate as quickly as that of the larger fish (Fig. 7) because of the relative constancy of the planting levels (Table 2). The fish move quickly through the smaller sizes and the accumulative effect of the plantings becomes more apparent with more time at large. The increases in average weight of the fish sampled (top line, Fig. 7) were influenced by the efficiency (Hamley and Regier 1973) and selectivity of the various gillnet mesh sizes used, but neither of these effects influenced the rates of change for the individual size-classes.

Diet Composition

That the survival and growth of lake trout had not yet (to 1984) been impeded by food shortages suggested on the one hand that the stocks were not at imminent risk. The reductions in sculpin and smelt abundance, and in alewife average age (Figs.

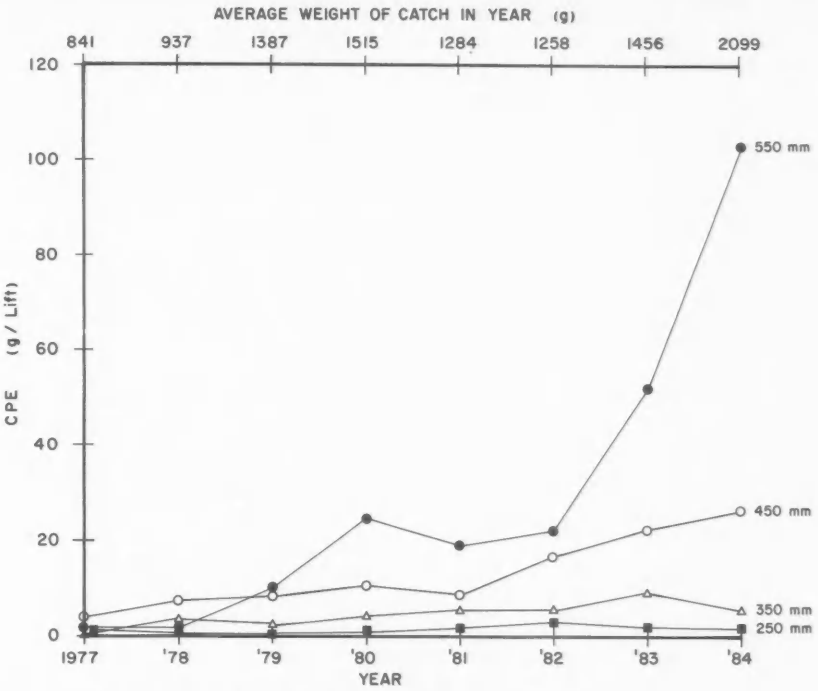

FIG. 7. Size composition of annual lake trout collections, Kingston basin.

2, 3, 4), on the other hand, suggest that the effects of prey limitation may not be long in emerging in the trout stock. In the following we examine qualitative and quantitative aspects of trout feeding for further symptoms of the limitation.

There have been changes in the diet of lake trout in Lake Ontario and they reflect in a general way the changes in the fish community. Dymond (1928) examined a sample of trout taken by the commercial fishery at the west end of the lake. He found that alewife were frequently eaten in the spring but were partially replaced in the diet by the deepwater ciscoes (*Coregonus* sp.) in summer because the alewife were less available during their inshore spawning migration. Smelt did not occur in the samples because they had not yet become established in the lake at that time (Christie 1972). Both the deepwater sculpin (*Myoxocephalus thompsoni*) which disappeared in the 1950's (Christie 1972) and the slimy sculpin were found in the trout stomachs. These observations contrast (Table 3) with recent samplings in the same area of the lake by way of the absence of the deepwater sculpin and ciscoes and the dominant position of the smelt in the trout diet. Dymond's sample consisted of trout averaging 3.9 kg, with few fish smaller than 2 kg, while recent observations include smaller trout as well. This accounts in part for the large numbers of slimy sculpin in the recent observations (see below), but it does not affect the generalization that slimy sculpin and smelt have replaced deepwater sculpin and ciscoes in the recent summer diet.

The western Lake Ontario observations suggest further that in recent years the trout stocked there have relied more on slimy sculpin and smelt, while the Kingston basin fish have used alewife, smelt, and sculpin in generally equal proportions.

Observations from the Kingston basin show that the smelt and alewife increased in the diet by about the same proportions between the two sampling periods, while the sculpin frequency of occurrence declined by about 50%. These changes are consistent with both the expansion of the size composition of the trout population in the recent period and the changes in prey stock densities.

The only other species that have been regularly observed in the trout stomachs are the trout-perch and johnny darter, and both have occurred less frequently lately. No invertebrates were found in the trout stomachs in either of the study periods, so the trout evidently adjust to piscivory upon their release as yearling fish (approximately 150 mm). That no increase in diet diversity has occurred offers further support for the contention that food levels were not a limiting resource for the trout through this observation series. When food does become limiting, it is likely that diversity of diet will increase as a result of increased utilization of invertebrates, darters, and trout-perch and possibly also by way of intensified summer foraging for warmwater fish outside the normal thermal range of the trout.

A first hypothesis that lake trout feed opportunistically on whatever fish are available in their habitat can be rejected because the trout of different sizes are demonstrably selective for different prey species (Fig. 8).

All species are included in the diets of all trout sizes, but small trout select sculpin and move to smelt and alewife at progressively larger sizes. The greatest harvest pressure on the sculpin stocks is exerted by trout in the 250-mm size-class. The biomass of this size-class of trout has changed least since the beginning of the sampling series (Fig. 7), and this has somewhat protected the sculpins from the constantly rising predation pressure to which the other two species have been subjected.

The selection of the larger prey species by larger trout (Fig. 8; Table 3) in the recent data raises the possibility that the process

TABLE 3. Summary of lake trout food habit observations in Lake Ontario.

	South of Toronto				Kingston basin			
	1927[a]		1978–84		1957–66		1874–84	
Species	No.[b]	%[c]	No.	%	No.	%	No.	%
Alewife	85	66.4	50	7.2	43	11.1	918	28.4
Smelt			260	37.6	45	11.7	1148	35.5
Cisco	40	31.2						
Deepwater sculpin	16	12.5						
Slimy sculpin	5	3.9	381	35.1	268	69.4	1139	35.3
Threespine stickleback	1	0.8						
Round whitefish	1	0.8						
Trout-perch					4	1.0	14	0.4
Johnny darter			1	0.1	26	6.7	9	0.3
Yellow perch							3	0.1
Total stomachs examined	272		1882		925		5273	

[a]From Dymond (1928) for June 7 – August 23.
[b]Number of prey fish counted.
[c]Percentage of stomachs containing prey species. Total exceeds 100% because of multiple occurrence.

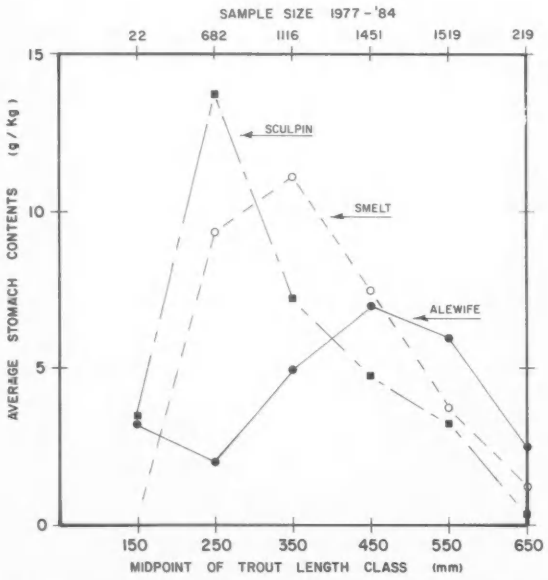

FIG. 8. Prey size selection by Kingston basin lake trout relative to sizes of the same species in trawl catches. Stomach samples of sculpin refer to 200–299 mm trout, smelt to 300–399 mm trout, and alewife to 400–499 mm trout.

is at least partly determined by the predator to prey size ratios. Comparison of the average sizes of the trout which had eaten the three prey species (calculated as means for the polygons in Fig. 8) with the average lengths of individuals of the prey species found in the stomachs produced general predator to prey ratios of 0.19 for sculpin, 0.30 for smelt, and 0.27 for alewife. If prey size was the only factor involved in the composition of the diet, one would expect that the sculpin ratio would be more closely aligned with those for the other two species, and this may suggest a preference for the sculpin by trout.

It should be noted, however, that further increases in the average size of the trout in the population (Fig. 7) should decrease the ratios for all three prey species because of the absolute limits to their maximum sizes. There are two other considerations of interest.

The trout select for larger individuals within the prey species as they grow larger (Fig. 9). Note that, as in Fig. 8, the data are means of annual averages to approximate midseries conditions in the size compositions of the prey species. The comparable slopes of the three lines in Fig. 9 suggest some generalized factor involved in the selection of larger prey by larger predators. The different body shapes of alewife and smelt of the same length, and the much smaller body size of sculpin, seem to rule out the possibility that this factor can be the mouth gape of the trout.

The other point is that the sculpin taken by the trout span more of the whole range of sizes in the sculpin population (56%) than do the smelt and alewife in relation to their population ranges (34%). This indicates that the sculpin are available to the trout in a broad range of life stages, while the younger alewife and smelt in particular are not so readily available.

The contribution of smelt to the diet was variable through time (Table 4), but without any lasting trend, while the alewife became more important and the sculpin less important in the trout diet. With rising trout biomass through the observational series, the values all represent rising harvests from the prey resources. The variations between years (Table 4) reflect diet shifts related to variations in prey size and abundance, and possibly shifts in diet preference as well. Full analysis of these effects is beyond the scope of the present article.

A further indication that the lake trout had not encountered food limitation at least up to 1984 is found in the fact that the averages for the total weights of the stomach inclusions do not show consistent decline in any of the lake trout size-classes. The example given in Table 4, for 400–499 mm trout (right-hand column) indicates an average reduction of 19.4% between the averages for the first four and second four years of the series, but this was due to the unexplained high values measured in 1977 and 1980. The difference between the sets is not statistically significant ($P \gg 0.05$). Moreover, the other six values are

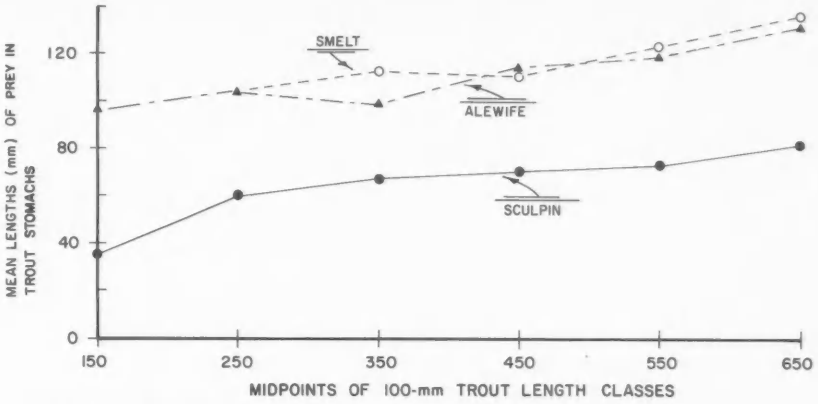

FIG. 9. Sizes of fish eaten by Kingston basin lake trout. Sizes were averaged over 1977–84 by trout size class.

TABLE 4. Food habits of lake trout in eastern Lake Ontario. Midsummer averages for 400–499 mm trout.

Year	No. of trout examined	Stomach contents (g/kg trout)			
		Alewife	Smelt	Sculpin	Total
1977	67	6.25	3.34	10.32	19.91
1978	206	1.81	3.89	5.49	11.19
1979	200	1.28	6.86	3.99	12.13
1980	177	6.34	6.96	3.22	16.52
1981	150	5.85	3.89	2.04	11.78
1982	62	2.63	6.66	1.29	10.58
1983	289	7.13	5.10	1.18	13.41
1984	178	8.44	3.49	0.45	12.38

without trend and are closely clustered (the coefficient of variation is 6.7%).

The sizes of fish found in the lake trout stomachs tend to be smaller than those sampled in the companion bottom trawling (Fig. 10). In the case of the sculpin, we suspect that smaller fish are associated with rocky bottoms where the trawl cannot be operated, but trout predation occurs. With the smelt, it is more likely that the trout forage higher into the water column than the trawl reaches, thus tapping strata of smaller fish. Through six of the eight years, however, variations in the sizes of smelt eaten reflected changes in the size composition of the smelt population sampled by the bottom trawl. Sampling error cannot be ruled out, but the large relative sizes of smelt measured from the trout stomachs in 1977 and 1980 (Fig. 10) could have resulted from behavioural effects, such as preference (for sculpin in 1977), habituation (in seeking out alewife in 1980), or aversion (related to avoidance of the abundant small smelt in 1980). These observations suggest, in general, that lake trout preferred to feed near the bottom. This is consistent with the sequence of predation impact (Fig. 2, 3, 4) which showed effects first in the sculpin, next in the smelt, and finally in the more pelagically distributed alewife.

The sizes of alewife consumed by the lake trout were also smaller than those collected by trawling (Fig. 10), but there is no evidence of correlation between the two data sets. The measurements of alewives from the stomachs varied 43% between the least and greatest annual averages, while the larger fish taken by

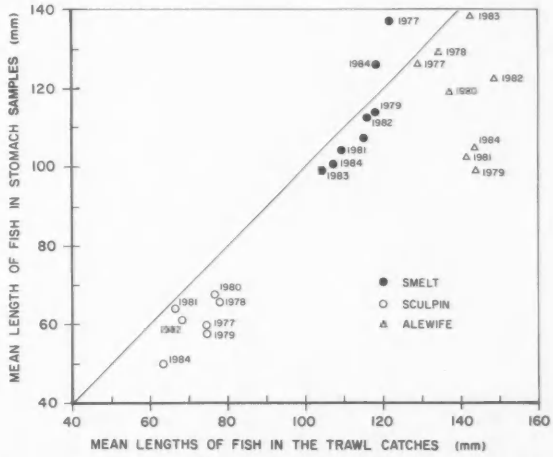

FIG. 10. Comparison of the quantities of three main prey fishes in the diets of Kingston basin lake trout of different sizes. Data are between-year averages for the period 1977–84 and refer to modal trout size classes used in Fig. 8.

the trawl varied only 10% (Fig. 10). This is consistent with an hypothesis that the trout capture alewife during forays away from the bottom. There is no explainable sequence in the annual averages for the sizes of alewife in the trout stomachs which can be linked to the abundance, size, condition, or age observations (Fig. 4). As we suggested in connection with the earlier discussion of year-to-year catch variance in the Kingston basin (Fig. 4), this observation begs answers to an important question about the factors involved in the summer vertical distribution of the alewife.

Discussion

The question emerging from this review of recent fish community composition changes in eastern Lake Ontario seems to be not whether predation has become an influencing factor, but rather where lake trout predation will lead in terms of future species abundances, and when important changes will occur. It seems unlikely that at present stocking levels, slimy sculpin will

be eliminated by lake trout. This is not so clearly the case with the smelt, where predation had evidently surpassed the compensatory capabilities of the stocks in recent years (1980–84). Smelt stocks persisted for years under substantial fishing pressure, but yield was constrained by the gillnet mesh sizes used, and the trout have likely been making deeper inroads into the stocks recently than the fishery did formerly by cropping juveniles as well as adults. Extinction of smelt is not impossible, and the present indicators predict at least a permanently reduced abundance for the species.

The alewife has so far been able to provide the additional food requirements necessary to meet the needs of the rising piscivore biomass, in spite of declines in the other prey species. The observed reduction in average age in recent years could be useful to the extent that an alewife population must be ecologically more efficient if it is not carrying large numbers of old, slow-growing fish. Equally, reduced competition from, and predation by, smelt could enhance alewife productivity.

Another positive outcome of an altered food chain would be reduction of the high levels of contaminants in trout flesh. Borgmann and Whittle (1983) suggested that the elevated levels in trout arose in part because of the nature of the *Pontoporeia*-sculpin benthic system they depended on. In discussing the high contaminant levels in *Pontoporeia*, they noted (p. 332):

> If the sedimenting material on which they (*Pontoporeia*) feed has a lower nutritional value than that consumed by other invertebrates, and it contains similar concentrations of sorbed contaminants, *Pontoporeia* would have to ingest larger amounts of PCB and DDT to achieve the same amount of growth as pelagic invertebrates. Their higher contaminant levels would then be passed on to sculpins, which also have higher PCB and DDT levels relative to their size, than, for example, smelt.

This introduces the possibility that decreased utilization of sculpins, coupled with increased dependence on the zooplankton–alewife system, could result in decreased contaminant levels in the lake trout. This response would have an even greater likelihood if the alewife stocks have faster turnover rates.

There is an important negative side to the food web shift, and in our view, it contains the elements which should be of chief concern to fish managers. First, the variability in alewife abundance and its susceptibility to natural climatic oscillations make it a questionable prey species on which to base an entire salmonid management system in Lake Ontario. Graham (1956) was the first to suggest that the relative growth of alewife in Lake Ontario placed severe constraints on its physiological scope for activity (Fry 1947) because of likely high metabolic costs in osmoregulation. This was offered in partial explanation of the extreme sensitivity of alewife to water temperature changes at our latitude. This suggests one reason for the failure of alewife to colonize Lake Ontario naturally during the approximately 10 000 yr since the retreat of the Wisconsin Glacier (Christie et al. 1987). The explosive colonization of Lake Michigan by alewife in the 1960's (Brown 1972), with its remarkable effects on the whole ecosystem, was generally accepted around that time as attributable to the grossly destructured condition of the fish community (Christie 1974). Subsequent work (Eck and Wells 1987; Meisner et al. (1987)) also raises the possibility that alewife have had a recent climatic advantage which may or may not be lasting. In Lake Ontario the "Twentieth Century Climatic Anomaly" (Lamb 1977) almost without question reduced the prospects of overwinter mortality for the alewife, yet they were unable to take advantage of any of the sequential extirpations of the native deepwater ciscoes, *Coregonus nigripinnis*, *C. reighardi*, *C. kiyi*, and *C. hoyi* (Christie 1972), with which they competed as planktivores.

The present predation pressure being exerted by lake trout, walleye, and cormorants must be considered unprecedented in the history of alewife in Lake Ontario. When the lake trout and burbot were at peak densities in the 1920 decade, neither the birds nor the walleye (Hurley and Christie 1977) were important, and the deepwater ciscoes and deepwater sculpin likely buffered the offshore predation impacts of lake trout and burbot on alewife by acting as alternative prey.

An alewife collapse would be a serious setback for the salmonid rehabilitation program, but in a way its implications are more serious for the walleye fishery. Since the lake trout are not yet self-sustaining, both the fishery and the stocking could be put in abeyance to allow the prey to recover, and drastic though such moves would be, the fisheries could become no worse than they were 10 yr ago, and moreover, they could be recovered. The high productivity of the walleye, on the other hand, could be seriously reduced if it were internalized to the biological economy of the Bay of Quinte in the absence of alewife, and what this could mean for the ongoing structure of the Bay fish community and its fish yields is quite unpredictable. Hurley and Christie (1977) discussed the possibility that the appearance of the large stock of fast-growing walleye in the mid-1940's resulted from a period of climatic conditions favourable for reproduction. The explanation is still viable, but this analysis raises the additional prospect that the walleye population increase could have been encouraged by the availability of alewife resources released after the declines in abundance of lake trout and burbot. The earlier productivity of the Bay of Quinte, in other words, may have been internalized, and much lower.

Avian piscivory could play an important role in further structural changes in the Kingston basin fish community. To the extent the commercial fishermen were correct in suggesting young lake trout were a major prey item of the birds (presumably in spring or fall), a lake trout biomass could be stabilized by reduction of recruitment of either natural or stocked fish by way of this predation and it could entail little change in the growth rate of the trout. Alternatively, if the alewife is the most important prey of the birds, then cormorant competition with lake trout and walleye could result in reduced growth of the trout so that biomass could be levelled, or reduced, while numerical abundance was not so constrained. Whichever is the case, the central issue is that the magnitude of the fish harvest by the cormorants is sufficiently large that the birds should be taken into account in ongoing management, and their status and ecological role should be subject to ongoing monitoring and study.

The question of the joint use of *Pontoporeia* by whitefish and slimy sculpin raises another issue about future food web changes. The whitefish of the Bay of Quinte were suppressed by the combined effects of overfishing and eutrophication (Hurley and Christie 1977). With both of these stresses relaxed, would a recovery of the whitefish act to suppress the abundance of sculpin, and thus the lake trout productivity, by way of reduced food availability? There is no answer for the question, but it emphasizes the interactive nature of the three primary species, walleye, lake trout and lake whitefish, and hopefully will

remind fishery managers that it will likely require special understanding to optimize yields simultaneously from all three species.

Another scenario of the future is that reduced smelt abundance will be the trigger necessary to allow the lake herring to return to higher levels of abundance. This, on the one hand, could be a significant new source of larger food particles for the lake trout and it could enhance the growth rate of the older animals. On the other hand, the lake herring are planktivorous competitors of the alewife, and, as noted earlier, the native coregonines may have a competitive advantage.

Further, there has been no experience so far with young lake trout of the year. The johnny darter, whose populations may not be adequately sampled because of mesh selection in the assessment gear, is one possible prey and the trout-perch is another. The opossum shrimp (*Mysis relicta*) could also be important, and this could affect lake trout distribution and, by way of food web connections, influence trout abundance and yield, as well.

The foregoing considerations are all conjectural, but they underscore one important inference to be drawn from this review. This is that the various initiatives in water quality and fishery management have restored a large biomass of piscivores to the system, and the final community structure which will emerge from the resultant contemporary system flux is scarcely predictable. This suggests two pieces of advice for management. The first is that efforts to control or direct the natural processes of fish community succession (for example by alewife conservation) could be counterproductive in the long the run (Christie et al. 1987). The second is that allowable yields should be regulated at very conservative levels in order to ensure that the successional processes are not hampered.

Unlike other members of the Great Lakes chain, fish community succession in Lake Ontario could stall at a level which requires permanent and expensive management intervention because of missing species. This should offer attractive inducement to management to attempt to reintroduce one, or more, of the extinct deepwater cisco taxa. Christie (1972) suggested that the transfer of solar energy received at the lake surface and of materials arriving at the perimeter may be inherently inefficient because of the loss of the vertical vectoring formerly accomplished by the cisco in the main trench of the lake and the coupled lateral vectoring by the trout and burbot. The idea of joint management of trout, walleye, cisco, and possibly deepwater sculpin to improve lake productivity, as well as to make the trout prey base more secure, is one which should be carefully studied by management.

This study has revealed a number of strengths and weaknesses of the assessment process. First, given the inherent variability of various fish stocks, there is obvious advantage to maintaining long data series. There is always temptation to seek more modern and efficient sampling methods, but this study demonstrates that whatever the deficiencies of the old methods, they should be replaced only after careful study, and preferably, full calibration with the new.

The data further illustrate the risk of assessment methods which are incautiously designed to serve the data requirements of the traditional models of modern fishing theory (cf. Ricker, 1975) in a dynamic rehabilitation context like the one described here. Standard bottom-oriented sampling gear did not sample smelt, alewife, and sculpin representatively in this example, and this frustrated confident measurement of relative abundance and mortality. Clearly, improved assessment methodologies for midwater sampling, and for sampling small fish which live on rocky substrates, are needed. It is equally clear that, as Hile (1954) suggested, the assumptions of constant natural mortality and catchability used in high seas fish stock models are probably always hard to support in the dynamic freshwater context, and this is doubly true in the rehabilitation situation described here. This is the case because natural mortality will inevitably change with changes in predator–prey ratios. The best way to index such changes is to make studies of food habits intrinsic to the stock assessment routines. It is also clear that assessment should be sufficiently flexible to respond to shifts in the food web, like the increase in the abundance of the piscivorous birds.

Acknowledgments

The data reported on here were all collected under the auspices of the Ontario Department of Lands and Forests and its successor agency (1974) the Ontario Ministry of Natural Resources. That such a comprehensive series of observations was possible over such a long period is a tribute to a number of administrators who believed in ecology. This group includes many individuals, but the leaders who were most influential were William J. K. Harkness, Norman S. Baldwin, and Kenneth H. Loftus, and we especially acknowledge their support. The vessel operations were the responsibility of Messrs. J. Rycroft (1958–66) and R. McIntosh (1967– 86). Both men were fishermen who had to submerge their ingrained propensities to improve their fishing efficiency with time, in the interest of this work. We appreciate the understanding it took to make this transition and thank them for dedicated and systematic work.

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Recent Changes in Lake Michigan's Fish Community and Their Probable Causes, With Emphasis on the Role of the Alewife (*Alosa pseudoharengus*)[1]

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Eck, G. W., and L. Wells. 1987. Recent changes in Lake Michigan's fish community and their probable causes, with emphasis on the role of the alewife (*Alosa pseudoharengus*). Can. J. Fish. Aquat. Sci. 44 (Suppl. 2): 53–60.

Major changes in fish populations occurred in Lake Michigan between the early 1970s and 1984. The abundance of lake trout (*Salvelinus namaycush*) and several nonnative species of salmonines increased greatly as a result of intensive stocking. The exotic alewife (*Alosa pseudoharengus*), which had proliferated to extremely high levels of abundance in the mid-1960s, declined, particularly in the early 1980s. We believe that the sharp decline in alewives in the 1980s was caused primarily by poor recruitment during the colder than normal years of 1976–82. Several of Lake Michigan's endemic species of fish appeared to be adversely affected by alewives: bloater (*Coregonus hoyi*), lake herring (*C. artedii*), emerald shiner (*Notropis atherinoides*), yellow perch (*Perca flavescens*), and deepwater sculpin (*Myoxocephalus thompsoni*), and possibly spoonhead sculpin (*Cottus ricei*). All declined when alewives were abundant, and those that did not become rare, i.e. the bloater, perch, and deepwater sculpin recovered when alewives declined. We present evidence suggesting that the mechanism by which alewives affect native species is not by competition for food, as has often been hypothesized, and discuss the possibility that it is predation on early life stages. Despite the decreased availability of alewives in the early 1980s, salmonines continued to eat mainly alewives. The highly abundant alternate prey species were eaten only sparingly, but alewives still may have been abundant enough to meet the forage requirements of salmonines. Two new exotics, the pink salmon (*Oncorhynchus gorbuscha*) and threespine stickleback (*Gasterosteus aculeatus*), increased in abundance in the 1980s, and could become detrimental (particularly the salmon) to other species.

Les populations de poisson du lac Michigan ont subi d'importantes modifications entre le début des années 1970 et l'année 1984. L'abondance du touladi (*Salvelinus namaycush*) et de plusieurs autres espèces de salmonidés non indigènes a augmenté de façon considérable suite à un ensemencement intensif. Le gaspareau (*Alosa pseudoharengus*) introduit, qui avait proliféré de façon extrêmement importante au milieu des années 1960, a vu sa population décliner, surtout au début des années 1980. Les auteurs sont d'avis que le déclin du gaspareau noté au cours des années 1980 s'explique surtout par un mauvais recrutement de 1976 à 1982, années plus froides que la normale. Les populations de plusieurs espèces de poissons indigènes du lac Michigan semblent avoir été affectées par le gaspareau, notamment celles du cisco de fumage (*Coregonus hoyi*), du cisco de lac (*C. artedii*), du méné émeraude (*Notropis atherinoides*), de la perchaude (*Perca flavescens*), du chabot de profondeur (*Myoxocephalus thompsoni*) et, peut-être, du chabot à tête plate (*Cottus ricei*). On a noté un déclin de toutes ces espèces correspondant au moment où le gaspareau était abondant. Celles qui ne sont pas devenues rares, à savoir le cisco de fumage, la perchaude et le chabot de profondeur, se sont rétablies lorsque la population de gaspareaux a décliné. Les auteurs présentent des faits portant à croire que le mécanisme par lequel le gaspareau nuit aux espèces indigènes n'est pas celui d'une concurrence pour la nourriture, comme on en a souvent fait l'hypothèse, et traitent de la possibilité qu'il s'agisse d'une prédation au cours des premières étapes du développement. Les salmonidés ont cependant continué à se nourrir surtout de gaspareaux en dépit de la moins grande disponibilité de ces derniers au début des années 1980. Les autres espèces de proies fortement abondantes n'étaient que rarement consommées, mais il est possible que les gaspareaux aient été suffisamment abondants pour satisfaire aux besoins des salmonidés. Deux espces étrangères, le saumon rose (*Oncorhynchus gorbuscha*) et l'épinoche à trois épines (*Gasterosteus aculeatus*) ont vu leur abondance s'accroître au cours des années 1980 et pourraient devenir nuisibles (surtout le saumon) aux autres espèces.

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Most native species in Lake Michigan's fish community declined sharply between the mid-1800s and 1970. These declines, and reasons for them, are discussed in Smith (1968, 1970) and Wells and McLain (1973). Selective commercial fishing was regarded as the most important factor in the declines before about 1940 and impacts of exotic fish species, specifically the sea lamprey (*Petromyzon marinus*) and the alewife (*Alosa pseudoharengus*), as most important during 1940–70.

The sea lamprey was first reported in Lake Michigan in 1936 and by the mid-1950s (with help from the commercial fishery) had exterminated the native lake trout (*Salvelinus namaycush*) and caused serious reductions in the abundance of other species such as the lake whitefish (*Coregonus clupeaformis*) and burbot (*Lota lota*). Effective control (by treatment of nursery streams with selective toxicants) that began in 1960 had reduced sea lamprey abundance greatly by the late 1960s, and lake whitefish and burbot populations had begun a recovery.

The alewife, first reported in Lake Michigan in 1949, had reached phenomenal abundance by the early 1960s and was having severe detrimental effects on the native bloater (*Coregonus hoyi*), yellow perch (*Perca flavescens*), deepwater sculpin (*Myoxocephalus thompsoni*), emerald shiner (*Notropis atherinoides*), and lake herring (*Coregonus artedii*) and on the exotic rainbow smelt (*Osmerus mordax*). The mechanism by which alewives adversely affected other species was not obvious. Competition with these species (including their larvae) for food and predation on their early life stages have been the most frequently offered hypotheses (Smith 1972; Wells and McLain 1973; Crowder 1980). An enormous die-off in the winter and spring of 1966–67 reduced alewife numbers dramatically (Brown 1968), but the species had rebounded somewhat by 1970 (Wells and McLain 1973).

We here describe changes in Lake Michigan's fish community that have occurred from the early 1970s to 1984 and present our views on the processes responsible for these changes; emphasis is on the alewife, owing to its extreme influence on community dynamics. Our discussion is focused primarily on Lake Michigan proper (i.e. the lake exclusive of Green Bay) and includes the species whose populations have changed conspicuously in recent decades. Some of the changes in abundance in 1970–84 have been as dramatic as those chronicled by Wells and McLain (1973). They have also been informative in that the patterns of decline and recovery evident among populations of various species helped to define the strengths of interaction, as well as modes of interaction, between species.

Data Collection

The discussions of recent changes in abundance of some of the species mentioned here (bloaters, alewives, rainbow smelt, slimy sculpins (*Cottus cognatus*), deepwater sculpins, and yellow perch) are based mainly on the results of fall bottom trawl surveys conducted by the U.S. Fish and Wildlife Service each year during 1973–84. (Sources of data for other species are mentioned in discussions of the individual species.) During the surveys, samples were taken at 9.2-m depth intervals from 9.2 to 92 m at each of eight index stations widely distributed in the lake (Fig. 1). The trawls, which were fished from the Service's R/V *Grayling* in the northern part of the lake and R/V *Cisco* in the southern part, each had a cod end of 1.27-cm (stretched) mesh and swept an area 8 m wide and an average of 1.7 m high. (Sampling procedures and trawl specifications were described in detail by Hatch et al. 1981.) In recording catches of alewives, bloaters, smelt, and yellow perch, young-of-the-year (YOY) were separated from older fish (here arbitrarily called "adults"). Changes in abundance of alewives, bloaters, and smelt refer primarily to the older fish, whereas changes in yellow perch refer primarily to YOYs. Adult yellow perch in Lake Michigan are difficult to sample representatively with trawls because they mainly occupy areas where the bottom is too rough for trawling; the young perch, however, can be effectively sampled with trawls because their distribution includes smooth-bottom areas. No life-stage separations were made for slimy and deepwater sculpins, but the young of these species were so small that few were retained by the trawls. Conclusions relative to trends in abundance were based on changes in catches per unit of effort (CPUE) (mean numbers taken per 10-min trawl tow) at all depths for alewives, bloaters, smelt, and slimy sculpins; at depths of 27 m and less for YOY yellow perch, which were uncommon in deeper areas; and at depths of 55 m and greater for deepwater sculpins, which were scarce in shallower areas.

FIG. 1. Lake Michigan, showing index stations.

Population Changes

Sea Lamprey

Through sustained control efforts, sea lamprey populations remained at generally low levels in the 1970s and early 1980s. Although they did increase substantially in the mid-1970s in the extreme northwestern part of the lake, their numbers were soon reduced by chemical treatment of several Green Bay tributaries, the sources of the infestation (GLFC 1982). Fluctuations in abundance otherwise were minor.

Salmonines

Among six salmonine species common in Lake Michigan in the early 1980s, only the native lake trout (*S. namaycush*) was ever present in significant numbers before the mid-1960s. After it had declined to extinction in 1956, attempts to rehabilitate the lake trout through heavy stocking began in 1965 (Wells and McLain 1973). The planting of five other salmonines, primarily coho salmon (*Oncorhynchus kisutch*), chinook salmon (*O. tshawytscha*), steelhead trout (*Salmo gairdneri*), and brown trout (*S. trutta*), but also including brook trout (*Salvelinus fontinalis*), was initiated within the next few years. The annual stocking continued in the 1980s. Significant natural reproduction of lake trout did not occur. Some of the other salmonines reproduced naturally to varying degrees, but their populations were maintained mainly by stocking. The salmonine populations that have resulted from the plantings have generally not been measured directly, but their trends in abundance should follow, at least roughly, the trends in annual stocking rates. On that basis, the abundance of salmonines in Lake Michigan climbed more or less steadily from 1965 to 1984 (Fig. 2). Total plantings increased from an annual average of 3.4 million during 1965–68 to 8.6 million during 1969–72, 12.1 million during 1973–77, and 15.4 million during 1978– 84. Proof of the great buildup of salmonine populations is shown by the sport catch of these fish, which reached well over 1 million annually in the early 1980s. These predators were sustained mainly by the abundant alewives, although other species, particularly rainbow smelt and (for lake trout only) slimy sculpins, were also important in the diet (Stewart et al. 1981; Eck and Wells 1983).

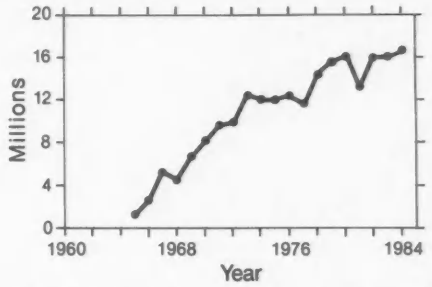

FIG. 2. Annual plantings of salmonines in Lake Michigan, 1965–84.

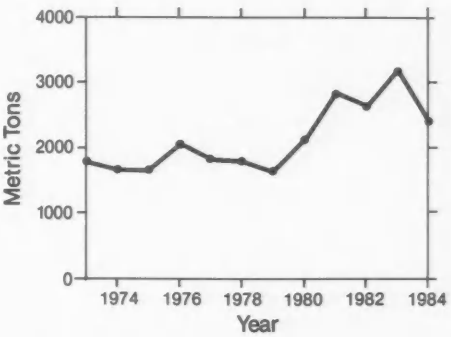

FIG. 3. Commercial catch of lake whitefish in Lake Michigan, 1973–84.

Lake Whitefish

Annual commercial production of lake whitefish (*C. clupeaformis*) in Lake Michigan held more or less steady at 1700–2000 t during 1973–79, increased rather rapidly to 3170 t in 1983, and dropped to about 2400 t in 1984 (Fig. 3). About 73% of the catch during 1973–79, and 83% during 1980–83, came from state of Michigan waters and nearly all the rest from Wisconsin. The extent to which the substantially greater lake whitefish catches in the early 1980s than in the mid- and late 1970s reflected increased abundance is difficult to determine. Production increased only in state of Michigan waters and actually declined in Wisconsin. Whitefish CPUE during the period do not seem to be useful indices of abundance. Between 1976 and 1983, in the major whitefish-producing waters of the state of Michigan, the CPUE increased 144% in gill nets, but changed little in trap nets. Although gillnet effort in that period declined 43%, and trapnet effort increased 52%, the proportion of the total take accounted for by gill nets remained about the same (30%). Regulation changes unquestionably influenced the CPUEs and total catches for both types of gear. Perhaps the most definitive statement that can safely be made is that whitefish in Lake Michigan became abundant in the mid-1970s and remained so in the early 1980s.

Burbot

The burbot (*L. lota*), which had recovered somewhat in Green Bay by the late 1960s following lakewide rarity in the early 1960s (Wells and McLain 1973), had begun to increase in the northern part of the lake proper by the mid-1970s according to reports of commercial fishermen. It had become common in the northern region by the early 1980s, but remained scarce (although increasing somewhat) in the southern region. Incidental catches of burbot in southeastern Lake Michigan, in standard graded-mesh gill nets set for lake trout, were 0.0 per 1000 m-night in 1971–74, 0.1 in 1975–79, and 0.7 in 1980–84 (National Fisheries Center – Great Lakes (NFC-GL), unpubl. data).

Forage Fish

Most forage species in Lake Michigan experienced striking abundance changes during 1973–84 (Fig. 4). Alewives and slimy sculpins were much less common at the end of the sampling period than earlier. Alewife abundance fluctuated with a modest downward trend during 1973–81 and then declined by a factor of six during 1981–83. Slimy sculpin populations increased from 1973 to 1976 but declined during 1976–84 (markedly between 1976 and 1977) to about 5% of the level of 1976. Bloaters, deepwater sculpins, and yellow perch were much more common at the end of the sampling period than at the beginning. The increase in bloater abundance began in the late 1970s and continued rapidly and steadily through the early 1980s (a more detailed description of recent changes in bloater populations is given in Brown et al. 1987). Populations of deepwater sculpins increased slowly from 1974 to 1978 and rapidly from 1978 to 1980 and then suffered a substantial decline in the early 1980s, from which they quickly recovered. The abundance increase of yellow perch occurred mainly in 1983, when an exceedingly strong year-class was produced; another strong year-class followed in 1984. Rainbow smelt populations were fairly stable during the sampling period. They held nearly constant during 1973–80, increased briefly, and then declined during 1982–84 to the levels of 1973–80.

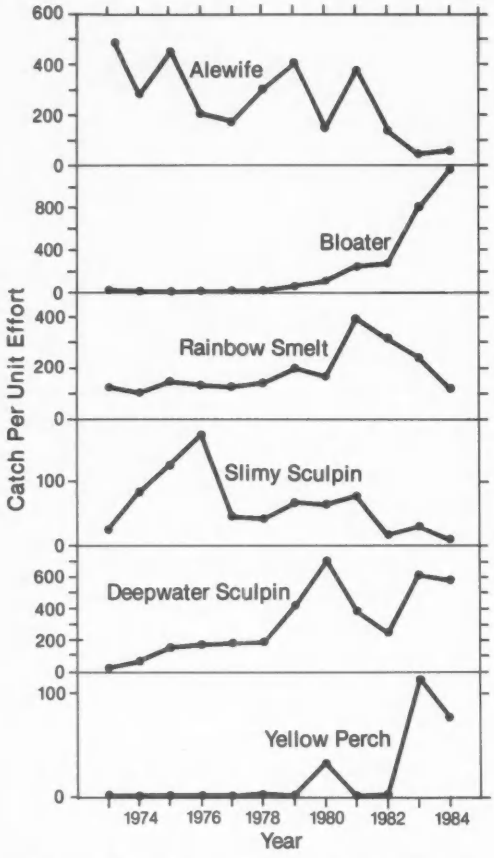

FIG. 4. Mean number of six forage species caught per 10-min trawl tow in Lake Michigan. Catches represent ≥age I fish for all species except yellow perch where catches are of YOY fish only.

Populations of several species changed little during 1973–84. Lake herring, emerald shiners, and spoonhead sculpins (*Cottus ricei*) all of which had declined to extremely low levels of abundance before the 1970s, remained scarce throughout the 1970s and early 1980s.

Reasons for the Changes

Several factors were involved in the changes in Lake Michigan's fish populations in the 1970s and early 1980s, as was true for the vast population fluctuations that occurred before 1970. In the following discussion of the causes for the recent changes, special consideration is given to the factors involved in the alewife decline, since this subject has been the center of considerable controversy (Eck and Brown 1985; Kitchell and Crowder 1986).

Nonforage Species

Abundance changes in all nonforage species under consideration here were made possible at least in part by control of sea lamprey populations. The dramatic population buildup of salmonines, of course, resulted mainly from the heavy stocking of these fish, but the increase was much more pronounced than it would have been had sea lamprey populations not been held in check through continued sea lamprey control efforts. Increased abundance (or at least maintenance of high population levels) of lake whitefish despite intense fishing pressure attests to the outstanding resiliency of the species, but almost surely could not have occurred without continued diminished sea lamprey numbers. The substantial increase of burbot in the northern section of Lake Michigan was probably the direct result of sea lamprey control. The slower recovery in the southern section may have been related to the extreme scarcity to which burbot had been reduced in that area before sea lamprey control began. Further expansion of burbot populations throughout the lake seems likely if sea lamprey numbers continue to be held at low levels.

Exotic Forage Species

Three hypotheses have been promulgated to account for the recent decline in alewife abundance (particularly in regard to the sharp decline in the early 1980s) in Lake Michigan: predation by salmonines (Stewart et al. 1981), competition with native planktivores (Crowder and Binkowski 1983), and temperature-related effects (Eck and Brown 1985). Of these, the competition hypothesis is perhaps the least tenable. Crowder and Binkowski (1983) suggested that alewives had a competitive advantage over bloaters when alewives were abundant, but that the advantage may have swung to favor bloaters when alewives were reduced in abundance and the abundance of bloaters increased. This hypothesis requires some other factor, such as predation or temperature-related effects, to reduce alewife numbers to a level low enough for a swing in competitive balance to occur. In addition, it ignores the fact that alewives established themselves in Lake Michigan from the late 1940s through the 1950s, when bloaters were extremely abundant (Wells and McLain 1973). If a competitive imbalance favoring bloaters over alewives existed that time, as the competition hypothesis tends to suggest, then alewives surely would not have been able to colonize the lake as rapidly and completely as they did.

Eck and Brown (1985) hypothesized that a series of colder than normal growing seasons from 1976 to 1982 was primarily responsible for the recent reduction in alewife abundance. They reasoned that colder than average growing seasons could reduce growth of YOY alewives, which would be detrimental to survival because overwinter survival of young alewives in Lake Michigan (Brown 1972), as in Lakes Huron (Argyle 1982) and Ontario (O'Gorman and Schneider 1986), is size specific, favoring the larger young.

To test this hypothesis, we examined the relation between alewife year-class strengths, derived from their contributions to trawl catches at age IV when they were fully vulnerable to the gear, and mean air temperature during each year-class's first growing season (July–October). We used air temperatures recorded by the National Weather Service at Muskegon, Michigan (NOAA 1969–79), because measurements of water temperatures from suitable lakewide locations and depths were not available. Average monthly water temperature taken from a depth of 13 m at the Muskegon Municipal Water Filtration Plant was, of course, highly correlated with Muskegon air temperature ($r = 0.99$, $P < 0.01$), using a 1-mo lag in water temperature to account for lags in heating and cooling.

The relation between alewife year-class strength and mean air

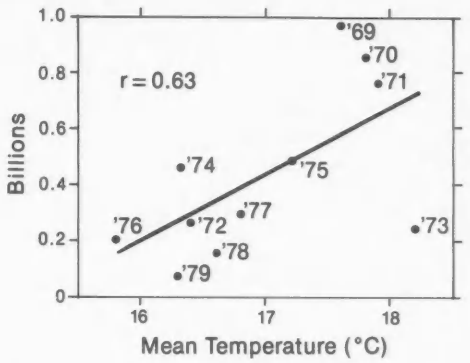

FIG. 5. Alewife year-class strength plotted against mean air temperature at Muskegon, Michigan, during the first growing season (July–October) of the year-class.

temperature during each year-class's first growing season (Fig. 5) was positive and significant ($r = 0.63$, 9 df, $P < 0.05$), suggesting that cooler growing seasons result in weaker alewife year-classes. During 1976–79, any poor survival of young resulting from cool growing seasons could have been exacerbated by the unusual severity of the winters in that period; the expected return period of three consecutive winters as abnormally cold across the contiguous United States as the winters of 1976–77 through 1978 -79 was estimated at 550–1010 yr depending on model assumptions (Karl et al. 1984). Mean winter air temperature at Muskegon, for example, averaged 2.5°C lower from 1976–77 to 1979–80 than from 1969–70 to 1975–76. In Lake Ontario, the severe winter of 1976–77 was suspected of contributing to the complete failure there of the 1976 alewife year-class (O'Gorman and Schneider 1986).

Stewart et al. (1981) used energetics-based population models to estimate alewife consumption by salmonines in Lake Michigan and suggested that steadily increasing planting rates (Fig. 2) would eventually result in a predation rate great enough to depress alewife stocks. They estimated that in some years as much as 33% of the biomass produced by age I and older alewives was eaten by salmonines and cautioned that an increase in alewife mortality that was independent of predation pressure, such as that caused by weather-related phenomena, could precipitate a drastic reduction in alewife abundance. More recently, however, Kitchell and Crowder (1986) have suggested that Stewart et al. (1981) underestimated the amount of alewives consumed and that predation may have been responsible entirely for the alewife decline.

Stewart et al. (1981) predicted that, if alewives declined due to increased predation, salmonine growth rate and condition should also decline (provided alternate forage was not available) and diet diversity should increase — obvious eventualities for predators that are overexploiting their primary prey. As evidence that this had occurred for salmonines in Lake Michigan, Kitchell and Crowder (1986) cited Hagar (1984) who reported that growth and condition for all salmonines had declined continuously since the 1960s. Hagar's findings, however, were based on incomplete data. A more rigorous statistical analysis of a complete data set (1969–84) rejected the hypothesis that salmonine growth or condition had declined in Lake Michigan (Hansen 1986). The only reduction in growth that Hansen substantiated for any trout or salmon species was in the maximum size attained by chinook salmon. He thus concluded that alewife abundance was not limiting salmonine growth at current planting rates, especially since the salmonines were still relying primarily on alewives for food (Hagar 1984). That salmonines have not exhibited widespread declines in growth or condition lends credence to the Eck and Brown (1985) hypothesis that the recent decline in alewife abundance was not induced by predation but was primarily a manifestation of climatic events instead.

Reasons are not obvious for the rather conspicuous increase in rainbow smelt abundance in 1981 or for the marked decline that followed in 1982–84, but the changes seem most likely to have resulted from normal fluctuations in year-class strength. Although rainbow smelt populations can be strongly affected by alewives when the latter are at extremely high densities such as they were in Lake Michigan in the early and mid-1960s (Smith 1970; Wells and McLain 1973), the fluctuations in smelt populations in the early 1980s obviously were not correlated with alewife abundance. The steady decrease in rainbow smelt abundance after 1981 suggested that a partial substitution of smelt for alewives in the diet of salmonines, as alewives became less common, had begun to depress the smelt populations. However, considerable tolerance of smelt populations to predation by salmonines is indicated by the smelt's establishment in Lake Michigan in 1923, and extremely rapid proliferation over the next two decades, despite an abundance of lake trout. Data regarding the extent of predation on smelt by lake trout are lacking for most of that period, but smelt were important in the diets of lake trout in the early 1940s (Van Oosten 1947), and probably in the earlier years as well.

Native Forage Species

Strong circumstantial evidence leaves little doubt that the dramatic increases in populations of bloaters and deepwater sculpins in the 1970s, and yellow perch in the 1980s, were related to diminished alewife abundance. Severe declines of these species that began in the early 1960s coincided with the rapid buildup of alewife populations (Smith 1970; Wells and McLain 1973). The direct cause of the decline in each case was poor reproduction, and as alewife numbers declined, reproduction by these species improved. Trends in reproduction of bloaters with changes in the abundance of alewives illustrate the relation. In the mid-1960s, when alewives were at peak abundance, the reproduction of bloaters was poor despite the presence of a sizable spawning population. But in the late 1970s, when alewife abundance had declined, bloater reproduction improved even though the spawning stocks then were small (Brown et al. 1987). During 1973–83, years for which lakewide data on reproduction are available, the abundance of YOY bloaters in fall showed a strong negative correlation ($r = -0.73$, 9 df, $P < 0.01$) with numbers of alewives (of ages fully vulnerable to the bottom trawl) in the previous fall, numbers that reflect the abundance of alewives in the preceding spring when the bloater larvae hatched (Fig. 6). How alewives interferred with bloater reproduction or adversely impacted other species is unclear, however.

There is some evidence to indicate that competition for food by alewives has not been an important factor in the declines of native fish populations in Lake Michigan. The growth rate of bloaters and yellow perch increased as alewife populations built up (Brown et al. 1987; Wells 1977), rather than decreasing as would be expected if they had been losing to alewives in

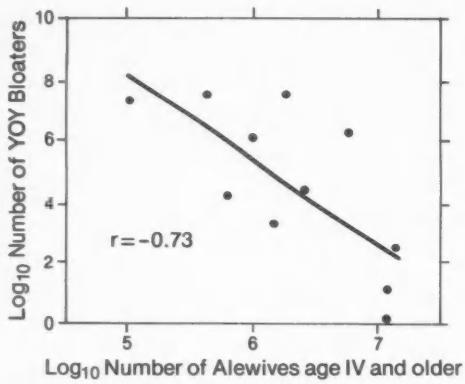

FIG. 6. Estimated number of YOY bloaters in Lake Michigan each fall 1974–83 plotted against estimated number of alewives fully vulnerable to the bottom trawl (i.e. ages IV and older) during the previous fall.

competition for food. (Data are lacking to follow changes in growth rates of other species as alewife abundance increased.) It could of course be argued that competition from alewives might have increased the mortality of larval bloaters and yellow perch by depriving them of food during the time when the larvae had absorbed most of their yolk sacs and were beginning to feed freely, a supposedly critical period in the survival of young fish. However, Rice (1985) showed that bloater larvae can be starved for several weeks without greatly increasing their mortality and that they then resume feeding when food becomes available. We do not know if yellow perch larvae go through a critical feeding stage, but even if they do, it seems doubtful that they suffered a food shortage at that stage. Food appears to have been much more abundant nearshore in southeastern Lake Michigan in the early 1970s, when alewives were abundant and year-classes of perch relatively weak, than in 1983 and 1984, when alewives had declined and perch year-classes were strong. According to Evans (1986), the abundance and biomass of nearshore zooplankton in southeastern Lake Michigan declined 90% between the early 1970s and 1983–84. Thus the diminished food supply in 1983—84, although probably causing the reduction that we observed in growth of the young yellow perch (NFC-GL, unpubl. data), obviously was still sufficient for survival of perch larvae.

Since alewives seem unlikely to have adversely affected native Lake Michigan species by competing with their larvae for food, they must have preyed on the larvae or eggs of the species that suffered declines when alewives became abundant. In Claytor Lake, Virginia, alewives are highly piscivorous, eating the larvae of at least six fish species, including yellow perch (Kohler and Ney 1980). Alewives 100–208 mm total length ate larvae 9–26 mm total length in Claytor Lake, and in another lake in the region, small alewives (80–85 mm) consumed larvae as long as 20 mm. Similar confirming evidence of alewife piscivory in Lake Michigan is lacking because appropriate food habits studies were not conducted when larvae of the species impacted by alewives were abundant.

Alewives had ample opportunity to feed on the larvae of the species that experienced poor reproduction in Lake Michigan when alewives were abundant. The larvae of all the species were in the presence of alewives at some time during their development (Wells 1966, 1968, 1974) and were small enough to be eaten by alewives (Auer 1982). They were also pelagic, and as suggested by Crowder (1980), fish eggs or larvae would have to be pelagic to be subject to much predation by alewives. Janssen (1978) showed that alewives were extremely inefficient at capturing prey that were on or near bottom. However, the degree of exposure to possible predation by alewives probably varied among species, depending on duration of their pelagic period and growth rate. This may account for the rapidity with which the lake herring, emerald shiner, and spoonhead sculpin disappeared from Lake Michigan after alewives became established (Wells and McLain 1973) and the differential rates of recovery of the bloater, deepwater sculpin, and yellow perch as alewives declined (Fig. 4). (Note: We infer that larval spoonhead sculpins are pelagic from their developmental pattern (Auer 1982) and the fact that spoonhead larvae were captured in oblique tows of a plankton net in Lake Superior (J. Selgeby, U.S. Fish and Wildlife Service, Ashland, WI, pers. comm.).)

The decline in deepwater sculpin populations in the early 1980s resulted at least in part from a die-off in the winter (and probably spring) of 1980–81. Trawl catches in spring 1981 contained many dead deepwater sculpins, a phenomenon not previously observed for this species in Lake Michigan (NFC-GL, unpubl. data).

The most logical explanation for the steady decline of slimy sculpins after 1975 seems to be predation by lake trout (the other salmonines eat few sculpins). Slimy sculpin larvae are not pelagic (NFC-GL, unpubl. data) and slimy sculpin abundance is not functionally related to the abundance of alewives (Fig. 4). Although certainly scarcer than they once were, slimy sculpins may have been more abundant than the trawl data of the early 1980s indicated. We (Eck and Wells 1986) found that slimy sculpins were often common in stomachs of lake trout caught in areas where trawl catches indicated that (at the time the trout were caught) few if any sculpins were present. This apparent anomaly probably relates to the low vulnerability of sculpins to the trawl during daylight. Brandt (1978) showed that in standardized trawl tows, catches of slimy sculpins may be 10 times as large at night as during the day, presumably because these fish are more active (i.e. less tightly on bottom, and thus more vulnerable to trawls) at night than during the day.

Discussion

The recent downward trend in alewife numbers has resulted in recoveries by some, but not all, species that declined dramatically when alewives were very abundant. Deepwater sculpins and bloaters may have regained their prealewife levels of abundance by the 1980s and yellow perch populations had improved greatly. Emerald shiners, lake herring, and spoonhead sculpins, on the other hand, showed no sign of recovery and probably will not do so unless alewives become only a minor component of the fish community. Spoonhead sculpins in fact may have no chance of recovery because they may be extinct in Lake Michigan.

Although a further decline in Lake Michigan's alewife populations would doubtless benefit some native species, it might be detrimental to the salmonines, which now feed mainly on alewives. A scarcity of food for salmonines would jeopardize a valuable sport fishery, a prospect that is causing considerable concern among some fishery managers. Resource agencies of states bordering Lake Michigan are contemplating reductions in the numbers of salmonines stocked to lessen predation on alewives and thus conserve the population (Kitchell and Hewett 1987).

Further decreases in alewife numbers would not, however, necessarily create a critical food shortage for salmonines. Rainbow smelt, bloaters, and yellow perch are alternative forage species available now, and emerald shiners and lake herring may be available in the future. Smelt, which are already commonly eaten by salmonines, are abundant and might be used as food much more extensively. Yellow perch, which are increasing in abundance, are readily eaten by salmonines (NFC-GL, unpubl. data); such predation ordinarily occurs in spring or during upwellings in summer, when the nearshore waters occupied by perch are cold enough to be occupied also by salmonines. Bloaters are extremely abundant and could substantially offset an alewife scarcity. As mentioned earlier, salmonines have eaten bloaters only sparingly, but alewives are probably still abundant enough to largely meet their food requirements. If alewife populations fall much below current levels, salmonines will probably feed more heavily on bloaters.

A collapse of alewife populations and a return of native forage fish populations in Lake Michigan to prealewife levels would yield several benefits. Native species such as bloaters and lake herring are far more valuable than are alewives to the commercial fishery, and yellow perch are more valuable to both the commercial and the sport fisheries. Although the combined populations of native species and the nonnative smelt may not support as large a biomass of salmonines as the alewife might have if it had remained abundant (Eck and Brown 1985), they should provide at least a reasonably large forage base, and one that should be more stable than that provided by the temperature-sensitive alewife.

Even if populations of alewives were reduced to insignificant levels, problems with exotic fish in Lake Michigan may not have ended. The sea lamprey (populations of which have remained at about 10% of their former levels in Lake Michigan since effective control measures were begun in the mid-1960s) is a constant threat, necessitating the continuance of expensive treatments of its nursery streams with a chemical lampricide. Another exotic, the rainbow smelt, might react to a suppression of alewives by undergoing a population explosion that would be detrimental to native fish species. However, heavy predation on smelt by salmonines probably would prevent them from reaching such great abundance. A recent invader of Lake Michigan, the pink salmon (*Oncorhynchus gorbuscha*), might eventually become a problem for other species. It has spread to all the Great Lakes since its accidental introduction into Lake Superior in 1956 (Emery 1985), and was common in northern Lake Michigan in 1985, according to anglers' reports. Pink salmon would seem to have the potential to become much more abundant and widely distributed in Lake Michigan than they now are, and to become serious competitors with, and predators on, the young of several native species. Another recent invader, the threespine stickleback (*Gasterosteus aculeatus*), seems less likely to affect native species detrimentally, but the possibility that it will cannot be discounted. It was first observed in Lake Michigan in 1984 (Stedman and Bowen 1985) and has become firmly established in at least the northern region (NFC-GL, unpubl. data). We expect it to become increasingly abundant and expand its range.

Fishery scientists and managers must take steps to forestall future drastic, undesirable changes in Lake Michigan's fish community. The first of these steps should be that of upgrading interagency assessment programs so that smaller changes in community structure can be detected and a better understanding of species interactions gained. Better informed managers might then be able to apply management procedures in time to neutralize undesirable changes before they become calamatous.

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Influence of Various Sources of Error and Community Interactions on Quota Management of Fish Stocks

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We compare the performance of fishery control systems based on population and surplus production models. We show that the population method is superior to a surplus production method over a wide range of observational and structural error conditions. We also show that adaptive fishery control systems have potential to reduce uncertainty surrounding management of fisheries like the walleye (*Stizostedion vitreum vitreum*) fishery of western Lake Erie where unknown bias and error in harvest statistics combine with environmental variability to contribute substantial uncertainty to the quota derivation process.

Les auteurs comparent le rendement de systèmes de contrôle de la pêche basés sur des modèles de la population et de la production excédentaire. Ils montrent que le premier est supérieur au second en présence d'une large gamme de conditions d'observations et d'erreurs structurales. De plus, ils montrent que des systèmes flexibles de contrôle de la pêche peuvent réduire l'incertitude liée à la gestion des pêches comme la pêche du doré jaune (*Stizostedion vitreum vitreum*) dans les eaux occidentales du lac Érié où l'erreur systématique inconnue des statistiques sur les pêches, liée à la variabilité environnementale, apporte un niveau élevé d'incertitude au processus d'établissement des contingents.

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Use of quotas in fisheries management has become a widely accepted procedure. Examples of quota-regulated fisheries include many whale and other marine stocks, anadromous stocks, and numerous freshwater stocks. Although the simplicity of a quota concept may be appealing, rules for quota derivation are subject to great uncertainty. A resource manager wanting to set a quota for a stock must face variable quality and quantity of historical data for the stock, a wide variety of methods and data transformations for estimating quotas, and a bewildering array of possible optimization techniques.

We (Shuter and Koonce 1987) have recently reviewed these methods and compared the performance of a population method and a surplus production method of calculating quotas. Through Monte-Carlo simulations of a walleye (*Stizostedion vitreum vitreum*) stock in western Lake Erie, we explored the limitations inherent in the methods. In these analyses, we found that surplus production methods were more often likely to collapse a fish stock or fail to estimate quotas than were methods based on more detailed population models.

In this paper, we will extend these analyses to satisfy two purposes. First, although our previous results suggested that methods based on population models were superior to surplus production methods under all conditions, the differences could have been exaggerated by the methods of comparison. The population model requires estimation of many more parameters (age structure of catch, terminal fishing mortalities, estimates of natural mortality, etc.), and most of these were given without error in the previous comparisons. Therefore, we will systematically extend the effects of uncertainty on the performance of the methods. Second, both methods are extensions of traditional single-stock fisheries management. As such, they ignore possible error due to neglect of community interactions, and we will explore the implications of this structural error as well.

Methods of Analysis

In the following analyses, we will rely on the Monte-Carlo simulations of fishery management systems described elsewhere (Shuter and Koonce 1987). Table 1 summarizes the population model used to simulate walleye in Erie, and Fig. 1 represents the calculation sequence in the Monte-Carlo simulations. As before, the quota management system is imposed on the stock at the end of 20 yr of historical catch. From an historical data set, the control system estimates Q^{MSY}, F^{MSY}, and B^{MSY}, which are maximum sustainable yield, the constant fishing mortality that generates maximum sustainable yield, and the average biomass of a stock when fishing mortality is held at F^{MSY}, respectively. A quota is then set for the fishery in year 21, and the system continues to run for another 19 yr, estimating Q^{MSY}, F^{MSY}, and B^{MSY} each year from all of the accumulated data to date.

Fishery control systems can start with one of three possible exploitation histories and may rely on one of three policy choices for quota calculation. Exploitation histories are pulsed ($F = 1.0$ in years 1 and 11, $F = 0.05$ in other years of the first

TABLE 1. Detailed description of the population model of the western Lake Erie walleye stock. M is instantaneous natural mortality, F is instantaneous fishing mortality rate for fish fully vulnerable to the fishery, P_i is the fraction of age i fish which are sexually mature, N_i is the number of age i fish, S_j is the reproductive potential of the stock in year j, and R_{1j+1} is recruitment of new individuals to first age class in year $j + 1$.

Characteristic of model	Description
Age structure	10 age classes (ages 1–10); each age class characterized by number of individuals and total biomass
Natural mortality	$M = 0.218 \cdot \text{yr}^{-1}$ for all ages
Individual growth	Each age class characterized by weight (W_i, kg) of individual at start of year where W_1 to W_{10} have values of 0.15, 0.29, 0.43, 0.56, 0.68, 0.79, 0.90, 1.0, 1.1, and 1.2; growth over the year is exponential
Recruitment	$S_j = \sum_{i=1}^{10} p_i N_i$ where p_1 to p_{10} are 10, 0, 0.18, 1, 1, 1, 1, 1, 1, and 1; $R_{1,j+1} = 4.0 \cdot S_j \cdot \exp(-0.333 \times 10^{-6} \cdot S_j + V_r)$ where V_r is a normally distributed random variable with mean 0 and variance 0.64; recruitment occurs at start of the year
Fishery	Fishing begins at the start of the year and continues at a constant rate throughout the year; instantaneous fishing mortality rate for age i fish is $q_i F$ where q_1 to q_{10} are 0.065, 1, 1, 1, 1, 1, 1, 1, 1, and 1

20), underexploited (F increases annually from 0.05 in year 1 to 0.25 in year 20), and overexploited (F increases annually from 0.05 in year 1 to 1.55 in year 20). Policy choices represent various tactics of quota calculation each with its own risk characteristics (Shuter and Koonce 1987). The three used in these simulations are constant effort (quota varied from year to year such that F remains constant at estimated F^{MSY}), constant harvest (quota is given by estimate of MSY for stock), and variable effort (quota is varied from year to year such that $F = F^{\text{MSY}} * B/B^{\text{MSY}}$, also using estimated parameters).

From the wide variety of possible formulations, we chose one population and one surplus production model to compare. We selected the surplus production model and estimators from Uhler (1979, model 2). The population model was an age-structured model with a Ricker stock–recruitment relationship. We estimated abundance at age and catchability at age with a virtual population method. The virtual population method treated only 10 age groups over a 10-yr horizon. Estimation of stock–recruitment parameters relied on estimated adult abundance in year t and yearling abundance from year $t + 1$ for all complete cohorts. Contributions of incomplete cohorts to the estimate of stock–recruitment were weighted by the fraction that age groups represented in the 10-yr time horizon of the virtual population analysis. Terminal mortality estimates were derived from the last complete cohort, with arbitrary values provided initially. Only natural mortality and the age-specific maturity schedule were assumed constant in the population model.

We will represent the performance of the control system by four criteria. Each combination of system, estimation method, and error condition will be replicated 20 times, and these four criteria will be calculated from years 21 to 40 of the simulations. The four criteria are (1) mean and standard deviation of harvest accumulated over years 21–40, (2) mean and standard deviation of stock biomass in year 40, (3) average percentage of the time the stock spent in a state of collapse, and (4) average percentage of time that the method failed to calculate a quota.

We will examine two main types of error sources in these simulations. We first focus on errors associated with harvest statistics. Building on our previous characterization (Shuter and Koonce 1987) of the effects of variable ratio of process (random environmental effects on year class strength) to observation error (catch statistic errors), we will explore the implication of observation error on both catch and effort and the additional error of incorrect estimation of natural mortality. Throughout these assessments of observation error, we will preserve a ratio of process to observation error of 10:1.

The second type of error will concern structural errors in the fishery control system. These errors are structural because they derive from incorrect characterization of the regulation of the true population. The two methods of estimating quotas represent the managed stock in different ways, the population method being more detailed. To explore the implications of these errors, we will examine the effect of community interactions on both methods by introducing either time-varying natural mortality or changing stock–recruitment relationship during years 21–40 of the simulations.

Results

Combined catch and effort error affected the surplus production method (Table 2) more than the population method. To preserve the 10:1 ratio of process to observation error in these cases, we assumed that catch error was multiplicative:

$$C_t = (0.8) \cdot C \cdot e^{v}$$

where C is the true catch in year t and v is a normally distributed random variable with mean zero and standard deviation 0.05. We also assumed that effort error was multiplicative:

$$E_t = E \cdot e^{u}$$

where E is true effort in year t and u is a normally distributed random variable with mean zero and standard deviation 0.05. Like the simulations with error on catch only (Shuter and Koonce 1987), variable effort policies seem to perform better than constant effort policies across all exploitation histories (Table 2).

Estimates of natural mortality are difficult to obtain. Error in

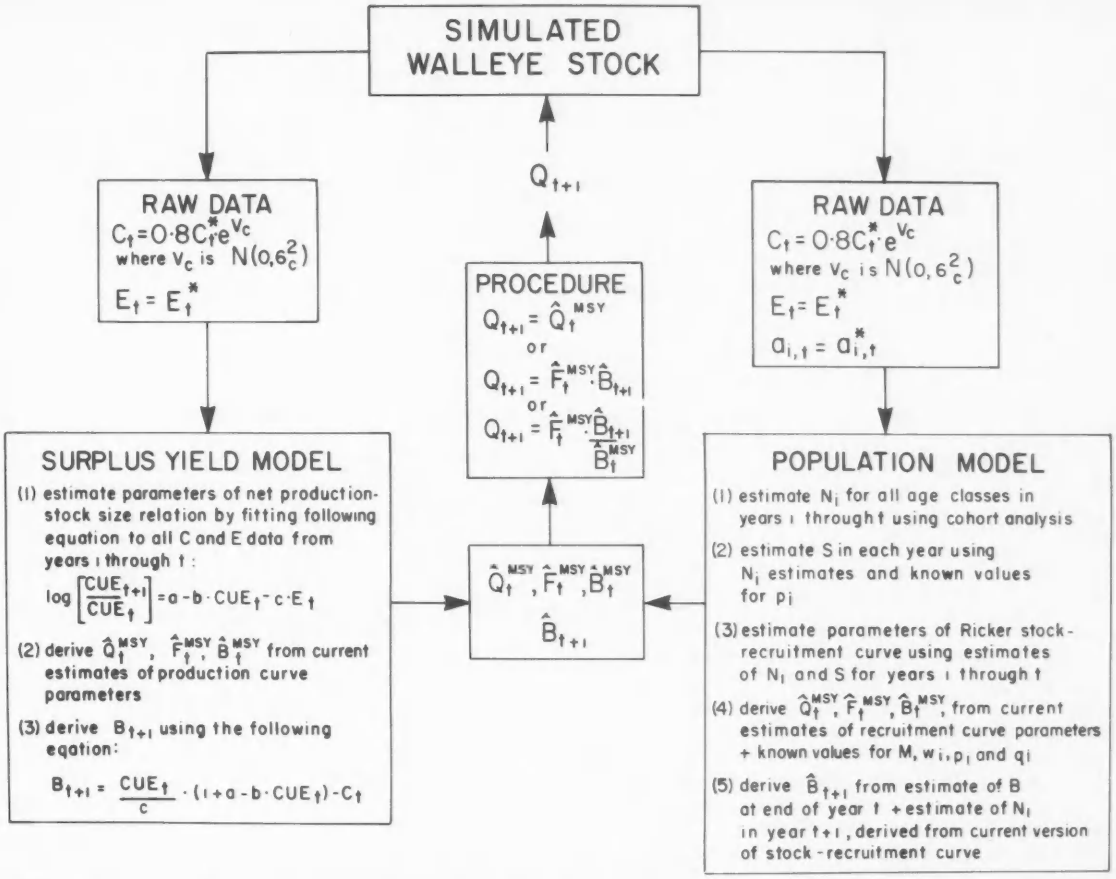

FIG. 1. Decision cycle of fishery control system followed for years 21–40 in simulations. On the left are steps followed for the surplus production (yield) model, and on the right are the steps for the population model. C_t is reported fishery catch in year t, C_t^* is true fishery catch in year t, E_t and E_t^* are reported and true effort in year t, $a_{i,t}$ and $a^*_{t,i}$ are reported and true value for the fraction of age i fish in the exploited segment of stock in year t, $CUE_t = C_t/E_t$, Q^{MSY}, F^{MSY}, and B^{MSY} are estimates of Q^{MSY}, F^{MSY}, and B^{MSY}, B_t is the estimate of fishable biomass at the start of year t, Q_t is the quota set for year t, and other terms are defined in Table 1.

this estimate affects both estimated state of the population and the optimal MSY parameter values. These influences, however, cancel each other, and the population method is not very sensitive to this source of error (Table 3). Underestimates of natural mortality (estimated natural mortality was 0.218 and true natural mortality varied from 0.3 to 0.5) did not lead to collapse of the walleye population. Overestimating natural mortality (true natural mortality was 0.218 and estimated natural mortality ranged from 0.3 to 0.5) led to problems only at very high overestimation (Table 3).

Structural errors, in contrast with parameter errors described above, occur because the models in the fishery control system are incorrect. Any model is incorrect at some level, so the important issue is sensitivity of the fishery control system to structural errors. Here, we explore two types of structural errors that mimic community interactions: systematic variation in natural mortality (e.g. invasion of a new predator) and systematic decrease in reproductive success (e.g. decreased survival of young-of-the-year caused by an unmodeled community interaction).

To illustrate the effects of unknown dynamics of natural mortality, we assume that natural mortality increases linearly from 0.218 in year 24 to 0.45 in year 35 of the simulations. Once more, the surplus production method is clearly inferior to the population method (Table 4). Harvests, as we expected, are generally lower than those in Table 2. Variable effort policies, however, are much better than constant effort policies for both methods. Not only do they yield higher harvests for the least risk of population collapse, but they end with a higher standing stock.

In contrast with unknown increases in natural mortality, decreases in survival of young-of-the-year cause optimal fishing mortality to decrease. The Ricker stock–recruitment function assumed in Table 1 has two parameters:

$$N_{,t+1} = A \cdot S_t \cdot e^{-B \cdot S}$$

where S_t is the adult abundance in year t and A and B are the parameters of the model. Here we assume that A changes from 4.0 in year 24 to 2.0 in year 35. This change corresponds to a 50% reduction in optimal fishing mortality but, like the

TABLE 2. Summary of selected results of Monte-Carlo simulations of the population and surplus production methods for various combinations of policy and exploitation history. These simulations assumed error in both catch and effort statistics.

History[a]	Policy[b]	Cumulative harvest (millions of kg) Mean	SD	Standing stock (millions of kg) Mean	SD	Percent time collapsed	Percent estimation failures
		Population method results					
P	CE	57.82	15.18	5.13	2.85	0.00	0.00
P	CH	33.26	11.54	6.14	6.29	16.50	0.00
P	VE	71.87	29.87	4.38	1.85	0.00	0.00
UE	CE	58.42	13.89	5.52	2.34	0.00	0.00
UE	CH	33.13	9.27	5.73	4.30	9.75	0.75
UE	VE	75.61	24.08	4.17	2.34	0.00	0.00
OE	CE	30.68	18.23	4.95	2.69	17.00	0.00
OE	CH	2.34	1.58	.00	.00	96.00	0.00
OE	VE	49.11	22.39	4.40	1.93	8.50	0.00
		Surplus production results					
P	CE	39.69	17.58	3.52	4.41	10.75	12.75
P	CH	16.97	3.71	.00	.00	78.75	0.00
P	VE	45.07	14.65	3.11	2.69	1.75	6.00
UE	CE	35.93	10.34	4.09	2.95	10.25	21.25
UE	CH	24.07	16.14	2.69	7.86	51.75	15.25
UE	VE	33.89	17.84	6.59	4.45	2.75	30.00
OE	CE	14.36	10.11	3.18	4.94	31.75	29.00
OE	CH	4.20	4.19	1.53	2.83	72.75	42.00
OE	VE	28.09	13.76	4.80	3.30	8.75	22.50

[a]P = pulsed; UE = underexploited; OE = overexploited.
[b]CE = constant effort; VE = variable effort; CH = constant harvest.

TABLE 3. Summary of selected results of Monte-Carlo simulations of the population model for various levels of error in the estimate of natural mortality. All simulations used the constant effort policy with a pulsed exploitation history. Error was assumed on catch and effort statistics.

M/M_t	Cumulative harvest (millions of kg) Mean	SD	Standing stock (millions of kg) Mean	SD	Percent time collapsed	Percent estimation failures
0.44	12.57	5.87	3.35	1.88	0.00	1.50
0.55	24.27	9.21	4.89	2.38	0.00	0.00
0.73	40.04	11.86	4.98	2.61	0.00	0.00
1.00	57.82	15.18	5.13	2.85	0.00	0.00
1.38	66.11	20.87	4.85	2.95	0.00	0.00
1.83	57.27	24.95	3.98	2.23	5.50	0.00
2.29	40.18	19.15	1.60	2.28	43.25	0.00

changing natural mortality simulations, did not result in diminished performance of the population method (Table 5). In fact, the same improvement of the variable effort policies observed in Table 4 also occurs in these simulations.

Discussion

Two findings of importance emerge from this and our previous study (Shuter and Koonce 1987). First, quota derivation using a detailed population model is preferable over a surplus production model in situations where the data are sufficient for use of either. Under the best circumstances, use of a surplus production model seems to run greater risk of fishery collapse and has persistent problems with parameter estimation. The assumptions of the model do not seem to be a major impediment. As Deriso (1980) has shown, detailed population models can be simplified to surplus production form, and the surplus production model and detailed population models are thus in some sense canonical. Parameter estimation, however, is fundamentally different in the two methods. Hilborn (1979) attributed these problems to insufficient contrast in a data set from which parameters for surplus production are estimated, and Ludwig and Walters (1985) have shown that even structurally incorrect two-parameter models produce better estimates of parameters than three-parameter surplus production models. In part, therefore, the basis for preference of a detailed population model in quota derivation rests on the way in which it sequentially estimates parameters.

The second key finding in this study is that management policies seeking to maximize sustainable yield can be applied despite substantial uncertainties. In stating this, we do not wish to minimize the seriousness of the debate about the wisdom of using policies based on maximum sustainable yield. Rather, if this is a policy goal, it does not have to be abandoned in the face of numerous sources of error. The effects of these sources of error can be understood, and in the case of management of walleye in western Lake Erie, the combination of errors seems to yield conservative harvest strategies (i.e. lower harvests with respect to maximum sustainable yield).

TABLE 4. Summary of selected results of Monte-Carlo simulations of the population (PM) and surplus production (SP) methods for variable effort and constant effort policies from a pulsed exploitation history. All simulations assume both catch and effort error with natural mortality increasing linearly from 0.218 in year 24 to 0.45 in year 35 and remaining at 0.45 through year 40.

Model	Policy	Cumulative harvest (millions of kg)		Standing stock (millions of kg)		Percent time collapsed	Percent estimation failures
		Mean	SD	Mean	SD		
PM	CE	45.18	12.59	2.10	1.73	0.00	0.00
PM	VE	52.46	17.08	2.52	1.16	0.00	0.00
SP	CE	31.04	12.98	1.36	1.94	15.00	12.50
SP	VE	34.34	7.33	1.54	1.16	4.50	0.00

Two factors contribute to the conservative characteristic of quota derivation. The first, of course, is the assumption that catch is underreported. Population state estimated from these data may, if the value assumed for natural mortality is greater than or equal to the true value, be less than the true state, resulting in an actual mortality lower than intended. The second factor, which we believe to be more important, stems from the problem of errors in variables of the regression used to estimate parameters. Walters and Ludwig (1981) and Ludwig and Walters (1981) showed that this problem can create bias in parameter estimates. Using their guidelines, for example, Koonce and Shuter (1983) used simulations to show that estimates of optimal fishing mortality for yellow perch (*Perca flavescens*) and walleye in Lake Erie are, in fact, lower than the true optimum.

A less encouraging result that both methods share is the difficulty they have estimating true parameter values. The trends of estimated optimal fishing mortality for various error conditions illustrate this well. Given the population description in Table 1, optimal fishing mortality would be 0.42 for the population method and (because the Schaefer model assumes that the entire population is fishable) 0.20 for the surplus production method. Using these "true" values as references, convergence properties varied with method, policy, and history of exploitation (Fig. 2 and 3). Constant effort policies showed the best convergence of estimated optimal fishing mortality for the population method (Fig. 2A), and the variable effort policy was better for the surplus production method (Fig. 2B). Analyzing the better performing variable effort policies of the population method, we found that exploitation history generally resulted in convergence to higher than optimum estimates for underexploited populations or lower estimates for pulsed and overexploitation histories (Fig. 3A). All exploitation histories for surplus production methods based on a variable effort policy tended to overestimate true optimum exploitation (Fig. 3B). The prior history of exploitation, therefore, places substantial limits on the ability of a fishery control system to learn about the true state of the stock. From a management perspective, robustness of a model to error sources is thus a primary consideration in selecting combinations of exploitation policy and quota derivation method.

The learning properties of a control system, however, ultimately may be as important as their robustness to error. Ludwig and Walters (1981) showed that the information value of a fishery control measure increases away from the "optimum."

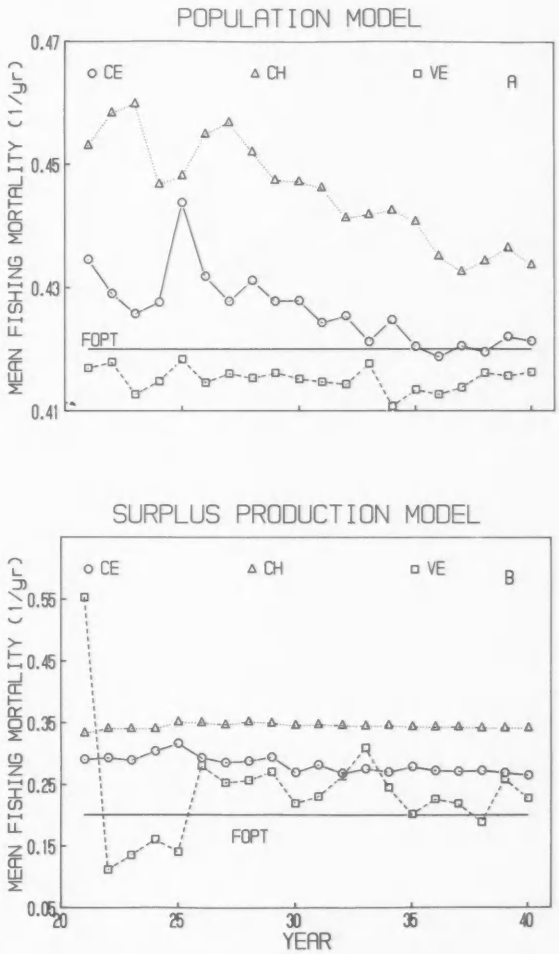

FIG. 2. Dynamics of mean fishing mortality during years 21–40 of the Monte-Carlo simulations for constant effort (CE), constant harvest (CH), and variable effort (VE) policies from a pulsed exploitation history. Panel A is for the (A) Population method; (B) surplus production method.

TABLE 5. Summary of selected results of Monte-Carlo simulations of the population and surplus production methods for variable effort and constant effort policies from a pulsed exploitation history. All simulations assume both catch and effort error with variation of the A parameter of the Ricker stock–recruitment relationship in Table 1. Remaining at 4.0 from years 1 to 24, A decreased linearly to 2.0 from year 25 to 35 and remained constant at 2.0 thereafter.

Model	Policy	Cumulative harvest (millions of kg) Mean	SD	Standing stock (millions of kg) Mean	SD	Percent time collapsed	Percent estimation failures
PM	CE	44.74	11.36	2.66	1.31	0.00	0.00
PM	VE	53.63	16.28	2.66	1.05	0.00	0.00
SP	CE	32.45	14.06	1.18	1.12	14.25	8.50
SP	VE	36.33	17.18	2.23	1.49	5.00	4.50

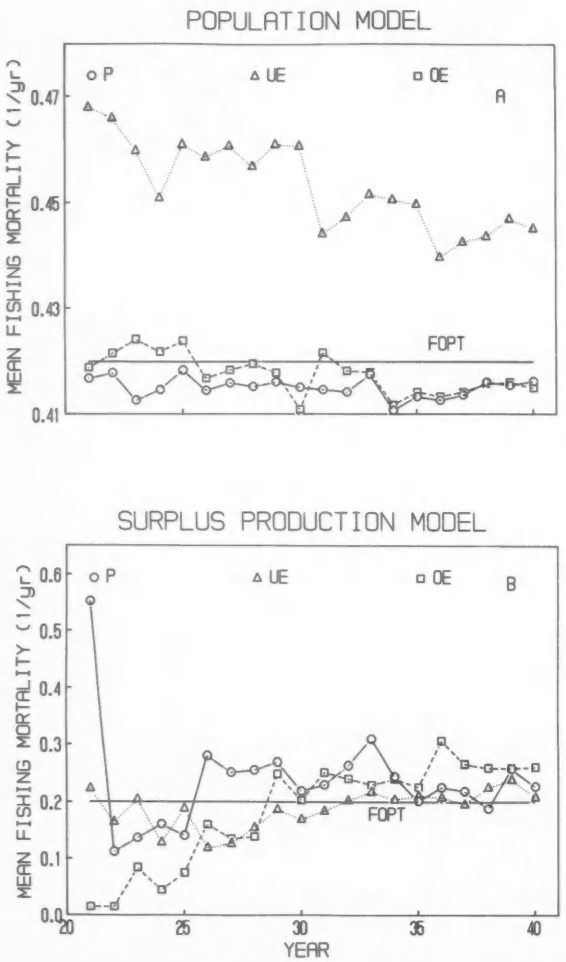

FIG. 3. Dynamics of mean fishing mortality during years 21–40 of the Monte-Carlo simulations for pulsed (P), underexploited (UE), and overexploited (OE) exploitation histories assuming a variable effort harvest policy. (A) Population method; (B) surplus production method.

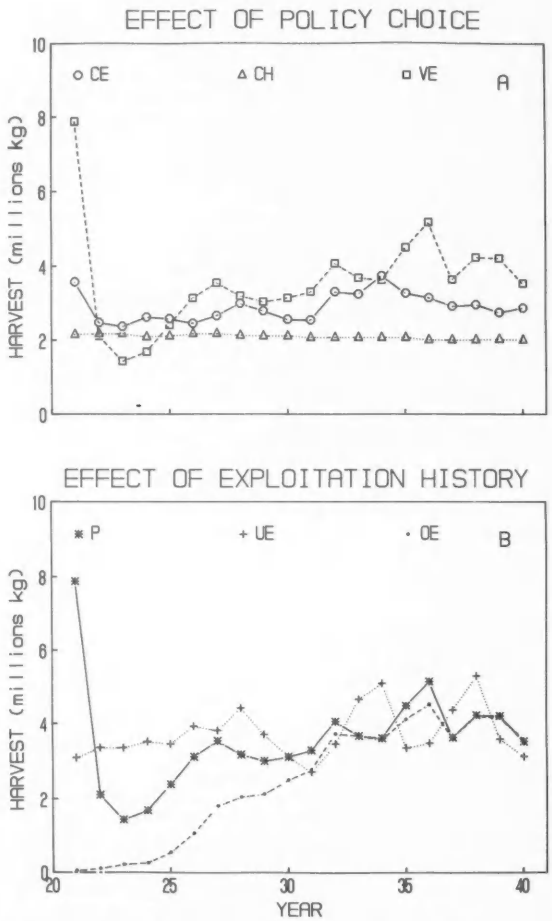

FIG. 4. (A) Dynamics of mean annual harvest of the population method assuming a pulsed exploitation history and various policy choices described in Fig. 2; (B) dynamics of mean annual harvest of the population method assuming a variable effort policy and various exploitation histories indicated in Fig. 3. Simulations included error on both catch and effort statistics.

The variable effort policies have this probing character (Fig. 3), but they do not affect parameter estimates as dramatically as the initial exploitation history. Given increasing evidence of nonstationarity of production relationships (Walters 1987), the slow convergence properties of these control systems (Fig. 2 and 3) severely limit their ability to "track" community changes. Nevertheless, exploitation histories and harvest policies that emphasize probing were qualitatively superior. Our selection of a pulsed fishing history, in fact, was motivated by indications from Ludwig and Walters (1981) that learning probes should be large to be effective. Variable effort policies, on average, do not seem to yield excessively variable harvests relative to other policies (Fig. 4A). The largest part of the difference in methods appears to be in the initial portions of the control process, and their exploitation history strongly influences the initial transients (Fig. 4B). Although the pulsed fishing history comes close to providing maximum contrast in the data set, it is undoubtedly impractical from a management perspective.

In generalizing our results, we want to emphasize two points. First, it is possible to establish some objective basis of preference for methods of quota derivation. We believe, however, that quota derivation must be viewed as a fishery control system (Fig. 1). If estimation of population state is uncoupled from the derivation of control parameters, various sources of error can become much more serious. The relative insensitivity of a fishery control system to estimates of natural mortality, for example, becomes a central problem in an uncoupled management scheme.

Second, use of more detailed representation of a population in the quota derivation scheme seems to yield better performance. In our population model, the advantage of detail was that estimation of quota ultimately depended only on two parameter estimates of the stock–recruitment relationship, a finding similarly reported by Ludwig and Walters (1985). In principle, community interactions could be expressed in terms of stock–recrutiment relationships, and it is tempting to speculate that incorporation of details of community interactions will enhance fishery control systems even more. This last promise, however, may be ephemeral. With realistic process and observation errors for walleye in western Lake Erie, even a structurally correct model does not obtain correct estimates of "true" parameter values. Furthermore, errors in estimation of natural mortality and underlying stock–recruitment relationship do not cause the fishery control system based on the population method to collapse the fishery. Actually, its performance is remarkably stable. Until process and observation error can be reduced, therefore, additional information on community interactions is not likely to improve fisheries management based on the kinds of fishery control systems that we have explored.

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An Ecological Approach to Fisheries Assessment

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Deductions based on recent ecological information suggest that while current fishery assessment methodology has captured the main features of fishery production, it may not well anticipate the effects of early natural mortality or of major changes in fishing. We propose here a new methodology based on ecological theory related to a characteristic biomass size spectrum. Theoretical considerations coupled with empirical data on population production appear to take into account high natural mortalities at small sizes and the effects of spatial distribution on production parameters throughout the life history. The resulting models offer a somewhat modified view of the relation of fishery yield to effort and the prospect of population assessments with more modest data requirements.

Des conclusions tirées de récentes données écologiques portent à croire que même si la méthode actuelle d'évaluation des pêches englobe les principales caractéristiques de la production halieutique, elle peut ne pas bien anticiper les incidences d'une mortalité naturelle précoce ou d'importants changements de la pêche. Les auteurs présentent une nouvelle méthode basée sur la théorie écologique relative à une gamme caractéristique de tailles de la biomasse. Des facteurs théoriques jumelés à des données empiriques sur la production démographique semblent tenir compte de taux élevés de mortalité naturelle des individus de petite taille et des incidences de la répartition spatiale sur les paramètres de production pendant tout le cycle vital. Les modèles obtenus offrent un exposé quelque peu modifié de la relation entre le rendement et l'effort et la possibilité d'évaluer des populations avec moins de données.

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Models underlying the assessment of potential fisheries production are intended to describe yield in terms of parameters subject to management manipulation or control. The Beverton and Holt (1957) formulation of yield-per-recruit in relation to size and fishing rate was a landmark of clarity, built on a respectable legacy of studies by Baranov (1918), Thompson and Bell (1934), Ricker (1940, 1945, 1954), and Schaefer (1954). Differences among these models have been chiefly in the handling of the production functions. However, as pointed out by Ricker (1975) in his discussions of Lee's phenomenon, certain obscurities have been persistent, and in general the models have not been satisfactorily comprehensive. For example, growth rate was sometimes considered as the equivalent of the aggregate of individual (physiological) growth rates, and sometimes as the net population (ecological) growth which took into account size-selective mortality. Nonfishing mortality has been generally treated as a constant. Recruitment functions, where they are considered explicitly at all, have fallen into two classes, the "average carrying capacity" or yield-per-recruit approach, which has low predictive capacity, or the more analytical "stock–recruitment" approach, which requires much data. Fishing mortality rates have also been treated as uniform within the gear-selection range and as exogenous variables which vary free from interactions with the rest of the system. The full consequences of these artifices have not yet been well appreciated.

Through experience with management, there has grown a confidence that the logical analytical systems developed for these partial models often predict short-term yield changes of the right order of magnitude. However, two problems have become more serious as fishing intensities have grown. The first is that the precision with which the manipulable parameters can be estimated is generally low, so that effective control of intensive fisheries in real-time terms is very demanding of costly data. The second is that the models lack an established basis either in ecology or in the socio-economic aspects of fisheries, so it is impossible to use them to extrapolate beyond the realm of present experience into suspected areas of critical interactions, or to help redefine long-term management policy objectives.

In response to these problems, there has been a renewed interest in the study of the properties of existing models, both to find relief from their insatiable data demands (e.g. Shepherd 1982a, 1982b) and to identify system properties which might support extrapolation (Allen and McGlade 1986). At the same time, information on ecological systems has been growing rapidly (Sheldon et al. 1977; Sprules 1980; Schwinghamer et al. 1986), leading to the speculative development of new production models (Platt and Denman 1977, 1978; Borgman 1982, 1983, 1987) in relation to certain properties of the component organisms. In this paper we offer an ecological rationale for assessment models, based on new information on the relation of body size in marine organisms to physiological and ecological scaling factors that underlie the rate of production. While the models we suggest are still in quite elementary form, the general ecological information on which they are based permits the development of exemplary production functions that depend

explicitly on life history aspects of growth and mortality of particular groups of species. We describe fish population yield models based on these relationships. The results provide a measure of the sensitivity of predicted yield to known ecological interactions and offer the prospect of more reliable extrapolation. If they can be verified, the generalizations would carry the supplementary benefit of reductions in data requirements.

Formulation of the Models

Earlier biological production models were constructed on the trophic level principle outlined explicitly in Lindeman (1942). Over a specified time period the yield C, to a predator at trophic level $n + 1$, from the average biomass B of a prey population at trophic level n, is expressed as

$$(1) \quad C_{n+1} = F_{n+1}\bar{B}_n$$

where C_{n+1} is the catch or yield to the predator, F_{n+1} is the fishing mortality rate generated by that predator, and $\bar{B}_n$ is the average biomass of the prey. The specific rate of production of the population (production per unit time per unit biomass) is defined as P_n/B_n, which in a stable population is equal to the total mortality rate, $Z_n = P_n/B_n = (F_{n+1} + M_n)$, where M_n represents population deaths that lead directly to the biological decomposition cycle. In addition, we define $P_n = K_n C_n$ where C_n is the food intake (catch) by the prey organisms from their own food supply at trophic level $n - 1$ and K_n is the gross production efficiency of food use by the population. Equation (1) can then be written in the form

$$C_{n+1} = F_{n+1}\frac{P_n}{Z_n} = F_{n+1}\frac{1}{Z_n}K_n C_n.$$

As pointed out by Dickie (1972), the ratio C_{n+1}/C_n is precisely the "ecological efficiency" as defined by Slobodkin (1963). Hence, by substitution and transposition, we define

$$(2) \quad \frac{C_{n+1}}{C_n} = F_{n+1}\left(\frac{B}{P}\right)_n K_n$$

or comparably

$$(3) \quad \frac{P_{n+1}}{P_n} = F_{n+1}\left(\frac{B}{P}\right)_n K_{n+1}.$$

That is, ecological efficiency or its related production efficiency, defined as the ratio of yields or productions in successive trophic levels, is a function of three parameters on which there is a growing body of information. Of equal importance is the fact that we may write in parallel with eq. (2) and (3) (Dickie 1976).

$$(4) \quad \frac{B_n}{B_{n-1}} = F_n\left(\frac{B}{P}\right)_n K_n.$$

That is, factors underlying ecological and production efficiency may be expressed in terms which are the equivalent of the ratio of the average biomass at two successive trophic levels. Expressing these important ecological ratios in terms of equivalent biomasses has the added advantage that the underlying variables are referable to a single trophic level, avoiding many of the difficulties and dangers of ambiguity in sampling and interpretation which arise in attempts to measure ecological efficiency directly. As pointed out by Dickie et al. (1987), the equations in this form make it possible to use current and growing information on the biomass size spectrum of bodies of water to deduce effects on yield in relation to specified features of the dynamics of the populations. In what follows, we describe features of the biological dynamics of populations which permit the fitting of these ratios as yield equations, leading to the assessment of yield potential, using accessible data.

Evaluating Parameters of the Biomass Spectrum

Application of the ecological equations to actual populations requires that there be stability in the observed stocks sufficient to permit estimation of parameter values from sampling. Stable population abundance appears to be a rarity in most fished stocks. However, Humphreys (1979) has shown that when species are considered in groups classified according to average body size, their production to respiration ratio per unit area of habitat is remarkably constant, and Banse and Mosher (1980) have shown that within similar groups the specific rate of production per unit area is significantly related to body size. Earlier, Ricker (1975) showed that, despite abundance fluctuations, when successive cohorts of fish are followed throughout their fishery history, catch curves of characteristic slopes can be constructed, and recent data suggest that survival rates of natural marine populations are under overall genetic control (Dickie et al. 1984; Doyle and Hunte 1981; Mallet et al. 1986). These findings, together with the more generally recognized stability of fishery yield despite fluctuations in the component species (Sutcliffe et al. 1977; Regier 1973; Pauly 1979; Holden 1978), give reason to suppose that realistically stable values of dynamic production parameters can be derived from stock data averaged over specified time periods.

Dickie et al. (1987) have reviewed the evidence for dependence of the parameters of the biomass spectrum (eq. 4) on body sizes of the component organisms rather than on trophic level. This evidence consists of a number of studies of the production efficiency, K, the specific rate of production, P/B, and the rate of mortality, F, on a unit area basis. Data compiled on many different natural populations of aquatic and terrestrial organisms have demonstrated a remarkable stability of these relationships with body size over many different environments and types of organisms, despite fluctuations in total abundance. For example, Humphreys' (1979) study of populations of 235 species of organisms established that when the species were classified into seven quasi-taxonomic (functional) groupings (three groups of poikilotherms and four of homeotherms), the net production efficiency was constant within groups. That is

$$(5) \quad P/R = a$$

where P is the rate of production and R is the rate of respiration per unit area. The parameter a takes different values for the different groups, but within groups is independent of body size, habitat, or the size of the production or respiration. In the data examined, all fish species fell within a single group.

In a parallel but independent study, Banse and Mosher (1980) found that when the various species were classified into groups, there was a remarkable constancy in the relation of the specific rate of production per unit area to the average body size of the component species. Their equation could be expressed in the form

$$(6) \quad \frac{P}{B} = bw^c$$

where w is body mass and the fitted expontial term, c, was constant at -0.37 within groups. The value of b differed among

groups, but again all fish species examined fell within a single group.

Schwinghamer et. al. (1986) studied additional groups of large and small species of invertebrates from the marine benthos and found that within two ecological groups, one a meiofauna group living in relation to the sand grains and the other a macrofauna group living in or on the substrate, the weight exponent of the P/B relation was approximately the same as that determined by Banse and Mosher (1980). However, if the ecological groupings were disregarded, the overall weight exponent was different, of the order of -0.2. Dickie et. al. (1987) pointed out that this is also true of the overall weight exponent derived from Banse and Mosher's data when the groupings are disregarded. They also pointed out that the overall weight exponent is not different from that derived by Hemmingsen (1960), which is accepted as reflecting the well-known physiological metabolic rate to body size relationship.

In a later study, Humphreys (1981) described the relationship between production and an index of prey utilization, within the same functional animal groupings studied earlier. These data amplify the Banse and Mosher findings and verify that within the groupings the weight exponent of specific production per unit area of natural habitat has a steeper negative slope than would be expected from a consideration only of physiological properties reflected in the rate of metabolism of the component animals, and may in fact have a somewhat steeper negative slope than was found by Banse and Mosher.

Taken together, these new considerations of the productivity of natural populations (i.e. per unit area of environment) suggest two important conclusions for the modelling of fisheries production. The first is that by specifying the body size of the organisms and the general functional grouping to which they belong, it is possible to evaluate the principal dynamic components of population production without the need to specify the trophic level. It appears in this connection that the general grouping to which an organism belongs is also specified by its body size.

The second major conclusion emerging from these studies is that the body size scaling of production is not a simple function of the physiologically determined metabolic rate in relation to body size. That is, the steeper negative slopes of the weight exponent within groupings of organisms apparently reflect specific features of the distribution of the living biomass in the environment (see also McGurk 1986). This distributional effect may well be termed an ecological scaling factor of production.

The interpretation and significance of the ecological scaling may be more readily appreciated if we juxtapose the Humphreys (1979) and Banse and Mosher (1980) conclusions in the identity equation

$$(7) \quad \frac{P}{R} = \frac{P}{B} \times \frac{B}{R} .$$

Since P/R is constant within a group and Banse and Mosher (1980) and Dickie et al. (1987) have shown that within such a group, $P/B = bw^c$ where c takes a value of about -0.4, it follows that B/R, which represents the biomass per unit respiration per unit area, must be related to individual organism weight by an exponent of about $+0.4$. This value is different from the value of about 0.2 which would be expected on the basis of the well-known relationship between metabolism and body size and appears to reflect size-related features of the biomass density distribution in natural populations. It may be related to the changing costs of predation and assimilation in populations of different average body sizes. These and similar relations that have been determined from studies of territoriality in grazing populations have been reviewed by Dickie et al. (1987), and their ubiquity attests to the generality of an ecological scaling factor in relation to body size. In fact, similar considerations of scaling in relation to body size apply to all three of the dynamic components underlying the efficiency ratios in eq. (2), (3), and (4).

It must be concluded from the foregoing that a primary scaling of production is related to physiological processes reflected in the overall relation of specific production parameters to body mass, $w^{-0.20}$ to $w^{-0.25}$. The secondary or ecological scaling factor which appears within groups of a limited average body size range is reflected in the within-species–group body mass exponent values of about $w^{-0.40}$. There is reason to suppose that a tertiary scaling may exist for ranges of body size within individual species. For example, McGurk (1986) has found that over their small size range the turnover rates of fish eggs and larvae have a mass exponent of over -0.8 and that this steep slope is at least partly explained as a result of spatial aggregations in their distribution. Similarly, Båmstedt and Skjoldal (1980) showed that RNA concentrations within species of zooplankton and small mesopelagic fishes have mass exponents of over -0.70 whereas exponents for interspecific comparisons based on average body sizes are described by a -0.33 value, comparable with that found by Banse and Mosher (1980). It thus appears that a third-order scaling may be required in dealing with production changes in relation to ranges in body size that are characteristic of cohorts of individual species, or at least the ranges of size within particular food and growth stanzas of the individual species (Paloheimo and Dickie 1966; Parker and Larkin 1959).

Fitting the Parameters in Fisheries Yield Models

The foregoing relationships enable us to use data on natural populations to establish values for modelling production and yield in terms of population growth and mortality.

Natural Mortality

If the age and size composition of any natural population is stable over a period of time, the various measured values of P/B for successive size groups are a measure of the average turnover rate at these sizes. That is, the specific rate of production at each size must be the rate of increase necessary to maintain the characteristic stock structure between sizes. In the long run, it would be expected that the observed growth rate has evolved as a result of the forces acting to produce this structure. Using such an argument, it could be concluded that an observed average growth curve is itself an indication of the natural mortality pattern which applies to the particular stock.

The foregoing argument will give an index of natural mortality for a fish stock only if it is known that growth rate has not changed due to fishing. However, since fishing effects seem likely to most influence the larger sizes, in which natural mortality is a relatively unimportant part of the total mortality, the argument might well be expected to be useful in exploring the effects of differences in prerecruit natural mortality patterns between stocks or species.

As an illustration of the method in the calculated examples, we have used growth curves and length–weight relationships for a population of herring (*Clupea harengus*) from the Scotian

TABLE 1. Age- and size-dependent production parameters for populations of herring and cod. $P/B = 1.05\ (\text{size})^{-0.37}$ (Banse and Mosher 1980) or $3.49\ (\text{size})^{-0.70}$ (Schwinghamer et al. 1986); $B/R = 0.887\ (\text{size})^{-0.37}$. (A) Herring population from southwest Nova Scotia after Tibbo (1957) and the condition factor $W = 0.005L^{3.3}$. Length at age 2 is interpolated. (B) Cod population from the North Sea after Daan (1974); $W = 0.007L^{3.1}$.

Age (yr)	Body length (cm)	Body size (cm)	P/B $c = -0.37$ (kcal)	P/B $c = -0.70$ (kcal)	B/R	B/R (rel.)
			(A) Herring			
0	—	1.4	0.931	2.779	1.000	0.146
1	11.0	10.5	0.440	0.672	2.118	0.309
2	23.0	119.9	0.179	0.122	5.212	0.760
3	28.8	251.8	0.136	0.073	6.859	1.000
4	29.8	278.7	0.131	0.068	7.121	1.038
5	31.9	352.8	0.120	0.057	7.771	1.133
6	32.8	386.7	0.116	0.054	8.039	1.172
7	33.7	422.9	0.112	0.051	8.309	1.211
8	34.1	439.7	0.110	0.049	8.430	1.229
9	35.7	511.5	0.104	0.044	8.915	1.300
			(B) Cod			
0	—	0.3	1.624	7.964	0.573	0.031
1	10	7.7	0.494	0.838	1.885	0.102
2	31	321.0	0.124	0.061	7.504	0.405
3	46	1180.7	0.077	0.025	12.150	0.656
4	65	3695.2	0.050	0.011	18.531	1.000
5	77	6463.2	0.041	0.008	22.790	1.230
6	85	8955.9	0.036	0.006	25.713	1.388
7	92	11628.6	0.033	0.005	28.322	1.528
8	100	15311.8	0.030	0.004	31.357	1.692
9	112	22255.9	0.026	0.003	36.011	1.943

Shelf (Tibbo 1957) and cod (*Gadus morhua*) from the North Sea (Daan 1974), together with egg size and fecundity data from Blaxter and Hunter (1982) and Oosthuizen and Daan (1974), to generate estimates of initial size (Table 1). In Fig. 1A and 1B, we show a resulting curve of mortality at age derived using the Banse and Mosher weight exponent of -0.37 and a higher value of -0.7, in keeping with the results of Båmstedt and Skjoldal (1980) and Dickie et al. (1987).

The natural mortality estimates depicted in Fig. 1 should correspond to a first approximation to equilibrium mortalities per unit area occupied by the stock. We cannot improve on them from the available data, in part because we lack information on the effects that changed fishing rates might exert on the rates of growth, through their influence on density. However, such effects should not seriously modify the difference in overall patterns of mortality for the two species, since both of them had been subjected to fishing for a number of years. The estimates may thus provide a first index of the sensitivity of yield changes to these important aspects of the population dynamics of types of species.

It is immediately evident from the figures that the natural mortality patterns for the cod and herring stocks are quite different from the rates typically used in current fisheries assessments, particularly for the smallest sizes. They are also different between species. However, the high levels of early mortality derived by this method are quite consistent with preliminary results of multispecies virtual population analysis (Gislason and Helgason 1985) and of mortality patterns based on bioenergetics considerations (Sissenwine 1985) that have been applied to similar production systems. These and other lines of recent evidence (e.g. Welch 1986) point to the probable importance of mortalities during postlarval and juvenile stages on the production characteristics of exploited stocks. In the present instance, the major difference between our method and that of others is that we have required relatively few data to reach similar conclusions. The approach appears to be applicable to most fisheries that have a characteristic biomass size spectrum and for which elementary size-at-age data are available.

Fishing Mortality

Current fishing theory defines the fishing mortality $F = qf$ where f is the number of effort units employed (number of boat days, for example) and q is the catchability coefficient, defined as the fraction of the total population removed by a unit of effort. While there is little real information on q, it is usually considered to rise rapidly in the threshold region of selection by the fishing gear and to be constant thereafter. The relationships deduced above suggest that an alternative formulation might be appropriate.

Fish are commonly found to be aggregated throughout the area of their occurrence, and a fishing vessel searches for areas of concentration within which it sweeps a given volume of water during each operation of its gear. Depending partly on the searching pattern, the search will cover a given volume of water per unit time. The fishing success will depend jointly on the total area over which the stock is distributed and on the probability of encountering a school during the search and fishing phases of its operation. If we suppose, as is reasonable, that the general area of occurrence of the stock is known from a combination of historical precedent and current fleet distribution, then the prob-

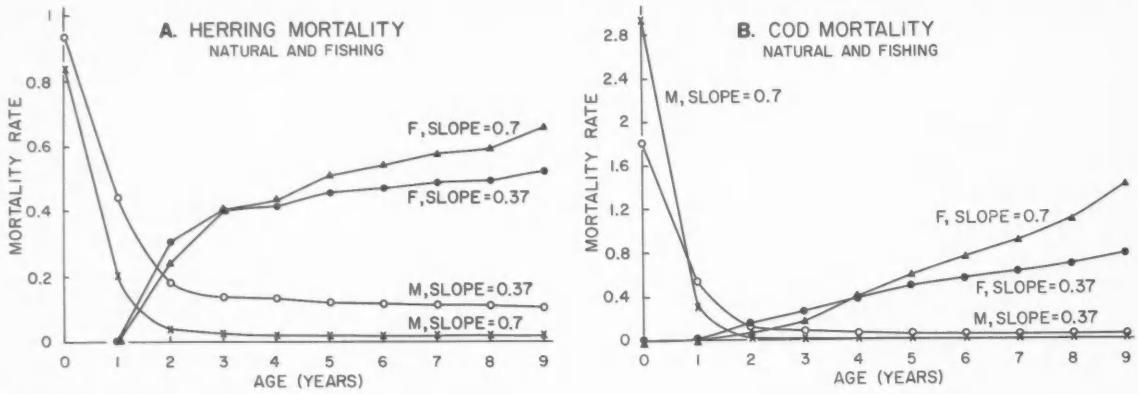

FIG. 1. Comparison of natural and fishing mortality estimates for (A) herring and (B) cod populations, described in Table 1, prepared using the two slope values described in the text.

ability of encountering and catching fish will be a function of the average population density and its variance. That is, the catchability of the fish population, q, is appropriately defined in relation to the probability of capturing a fish per unit area, rather than per unit population abundance.

It is in this connection that the foregoing ecological study of productivity is of particular interest. Dickie et al. (1987) have deduced that because of the combination of the physiological and ecological scaling factors underlying production, it is possible to define the ratio of biomass (B) to respiratory food requirements (R) in relation to the body size (w) of the feeding population. That is, within an area of given productivity, the total biomass which can be supported on a unit area will be proportional to B/R, which is itself proportional to $w^{0.4}$ or $w^{0.7}$, depending on the size range of population being considered.

Within a population on a given area, the abundance of a cohort at various sizes or ages is determined by a number of factors of recruitment and mortality. The relationship of B/R to w suggests that, given the relationships between size, food requirements, and biomass, as body size increases a higher proportion of the total biomass at that size can be supported on a given area. It follows that q defined in relation to population density should be proportional to B/R or to $w^{0.4}$ or $w^{0.7}$.

In Table 1 we have used an estimate of B/R to derive a relative value of q at different body sizes for the cod and herring populations. In the calculations, we have standardized q at age 3 for herring and age 4 for cod, based partly on the assumption that cod are on average recruited to fishing at a later age than are herring. The resulting yield curves are shown in Fig. 2 and are discussed in more detail below.

Recruitment

It is clear from eq. (4) that a period of relative stability of the population dynamics parameters corresponds to a period in which the biomass spectrum maintains a more or less constant form. In fact, we suppose with Borgmann (1982) and Platt and Denman (1977) that the populations being analyzed are characterized by such a size spectrum and that the populations which can be supported on a given food supply will be a function of that spectrum. While it is thus clear that considerable refinement may be possible, based on knowledge of the reproductive capacity of size elements in the stocks (Ware 1980), and the balance of stock and environmental influences on recruitment (Welch 1986), in the model considered here we make only the simple assumption that an upper limit of reproduction will be established by the living space made available by the growth and mortality of the stock. Such a reproduction function is comparable with a simple yield-per-recruit model and is reasonable for stocks in an equilibrium state. It may poorly approximate situations during periods of change in fishing or in intense fisheries. The possibility of delay-times in recruitment response, due to either stock or environmental influences, will then be of the utmost practical importance and require special consideration. It would appear from the foregoing that a study of the stability of the biomass spectrum for a region, both in total and by species, is likely to offer more direct and useful information than will any other data source. We do not consider such complications here, preferring to first examine sensitivity to the mortality formulations.

Relative Yield

It is evident from an explicit comparison of eq. (2) and (4) that conversion of the biomass spectrum to an ecological efficiency offers information only on relative yield changes, unless this is accompanied by information on the food supply and its uptake. It is often considered in population models that this is more or less constant, which is the same as assuming that K in eq. (2), (3), and (4) is a constant. Calow (1977) pointed out that within a given population this cannot be true for individuals on either theoretical or empirical grounds, although Borgmann (1982, 1983) has calculated an overall particle size conversion efficiency which suggests that it may be related to body size in a predictable fashion.

The nature of the population utilization of food by fishes was described by Paloheimo and Dickie (1966) in the form of what was termed the K-line. Kerr (1971) showed that it could be applied to natural populations by taking into account the size distribution of the prey population. Our use of observed growth data makes the relationship implicit, but it is reasonable to assume that the fish populations modelled here pass through two or more food stanzas, each characterized by a K-line applicable for the range of food particles taken in each stanza. This suggests that in addition to the initial recruitment to the first age group of the stock, there will be subsequent "recruitment" of the growing stocks from one stanza to another, depending on the availability of food as the population grows through its various

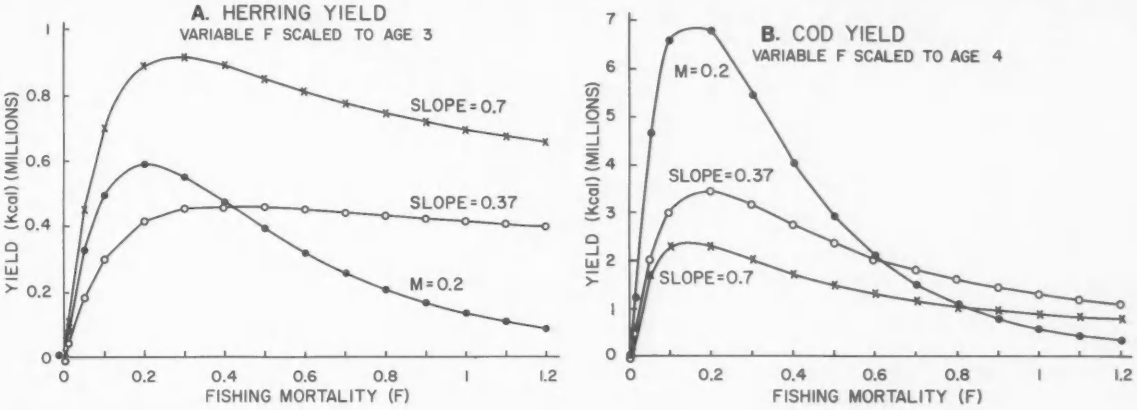

FIG. 2. Fishing yield per recruit estimates for (A) herring and (B) cod populations resulting from the mortality patterns shown in Fig. 1, assuming constant egg production, compared with yield estimated for constant natural mortality.

phases. Relevant observations on the prey resources of the populations analysed in Fig. 1 and 2 would provide a means for converting relative yield into terms of total population production.

Results of the Models

Examples of application of these "ecological" models with varying parameters to populations of herring and cod are given in Fig. 2A and 2B, respectively. The figures show predicted relative yield in relation to fishing intensity. For comparison, also shown are the results for constant parameter models, comparable with those used in current assessment techniques. The outstanding feature in both examples is the somewhat slower response of the yield to changes in fishing mortality for the varying parameter models, especially in the range of intermediate fishing intensities at F between 0.2 and 0.6. The difference is more marked for the cod example than for the herring.

It should be recognized that despite the superficial similarity in the results, there is a fundamental difference in the presentation which may eventually prove to have some practical importance. That is, the yield calculation for the more conventional constant parameter model implies that there is some whole population that is being exploited. The predicted steep drop in yield may thus be artificially exaggerated because of the implication that the population remains spread throughout its original area, even with large changes in equilibrium abundance. The variable parameter model involves a relative yield calculation which, because of the manner in which the P/B and B/R relationships are derived, is indexed on a per-unit-area basis. That is, the calculation of F in the variable model case takes into account changes in both the proportion of the original area occupied by the stocks and the efficiency of fishing.

The differences in yield are not, however, completely attributable to features of the fishing mortality description. This is evident at low fishing mortalities where the maximum yield and its rate of change in relation to fishing are different for the two species. Differences in these lower regions of the yield curves are more likely to reflect the differences in net population growth and mortality with fish size. Thus, for example, the highest yield of herring occurs at lower fishing intensities, and the rate of decline with increased fishing appears to be notably more gradual than with cod.

The level of relative yield, given in the figures in millions of kilocalories, is a direct result of the observed growth patterns, interacting with the fecundity and caloric determination data available in the literature. There are major apparent differences in the predicted level of yield for the two species which are suggestive of possible differences in unit area productivity. However, at the present primitive level of our calculation system, we are not in a position to evaluate their actual significance. The differences are related to the growth potentials of the species and the reproductive potentials of the environments, which are in turn expressed in features of the recruitment functions. The apparent yield differences result simply from insertion of different growth patterns in similar model systems. The usefulness of this approach is a subject for future specific study.

Discussion

It should not be surprising that the short-term changes in yield in relation to various fishing parameters deduced from these models do not differ substantially from the deductions of the simpler yield models which form the basis for current assessment of productive potential. Over the years the models in use have been successively calibrated and fine tuned by observing the results of management actions. The results show that current calculation systems have captured the main features of fish population production, and it is apprent that our calculations are in relative general agreement with them.

The main advantage which might accrue to practical management from model revisions remains, therefore, in the area of reliability of extrapolation from existing conditions and reduction in the high costs consequent on present dependence on large amounts of sample data. In the former area, it is evident from Fig. 1 that deductions based on recent ecological information imply that major changes in fishing practices may not be well anticipated by constant parameters, and this is verified in our model results. In the second area, our results support the implications of the even more general models of Borgmann (1982, 1983), and before him of Platt and Denman (1977) or Silvert and Platt (1980), which suggest that quite readily accessible information on the biomass – body size spectrum can provide practical and useful information. Our models have the possible advantage over these more general approaches in showing that by the addition of more explicit information on body size in

relation to various of the underlying production parameters, it may be possible to predict results at the level of individual species or the individual populations of species on which current fishery practice is based. The basic distinction is that our approach to mortality schedules is founded in ecological observation.

At this stage of analysis, the values of the weight exponents of the production parameters are still open to question. The values used in the paper are for illustration only. The reference material reviewed by both Humphreys and by Banse and Mosher has been assembled by them to provide comparisons *between* species, not *within* them, and the different exponents found by these authors may in fact reflect differences in the index of average species size that they adopted. Refinement of the models for application within species, such as we have undertaken here, is based on preliminary data and requires further studies of particular life histories. We do not yet know the extent to which this may vary between species having different life history energy strategies.

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A review of harvest theory and applications of optimal control theory in fisheries management[1,2]

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Cohen, Y. 1987. A Review of Harvest Theory and Applications of Optimal Control Theory in Fisheries Management. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 75–83.

Optimal control theory is a useful tool for analysis of general mathematical models of fisheries and harvest strategies. It provides a framework for management decisions, but is too general for direct application to many specific management problems. A review of applications of optimal control theory to fisheries management is presented, with a general audience in mind. Advantages and shortcomings of optimal control theory in the context of fisheries management are discussed with some specific examples.

La théorie du contrôle optimal constitue un outil utile pour l'analyse de modèles mathématiques généraux des pêches et des stratégies d'exploitation. Elle fournit une base pour les décisions relatives à la gestion mais elle est trop générale pour être appliquée directement à de nombreux problèmes de gestion déterminés. L'auteur présente, à l'intention du public, un examen des applications de cette théorie à la gestion halieutique. Il illustre à l'aide d'exemples ses avantages et ses inconvénients dans le contexte de la gestion halieutique.

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The following is a review of some results from the applications of optimal control theory to fisheries management. Since the intended audience is broad, I tried, wherever possible, to keep the presentation at an introductory level, limiting the discussion to analytical models only, and pointing out some useful results and pitfalls. One needs to keep in mind that most analytical models are gross simplifications of reality. Thus, they are useful for general understanding of dynamics of overriding importance in systems. The usefulness of analytical models to *specific* management problems is limited mostly to qualitative rather than quantitative insights.

The General Optimal Control Problem

Optimal control problems in ecology arise in cases where the conditions are complex: multiple input–output; constraints on state, input, and control variables; stochastic systems with potentially time varying parameters; large-scale systems with time delays; complications introduced by unknown "observer" effects; and distributed parameter systems. Derivations of optimal control policies from analytical models are based on the presumption that the simplified models capture some overriding mechanisms which govern the system. This often requires a leap of faith.

The starting point in formulating an optimal control problem is the first-order differential equations (distributed systems are discussed briefly later):

$$(1)\quad dx_i(t)/dt = f_i[x_1(t), \ldots, x_n(t), u_1(t), \ldots, u_r(t)]; \quad i = 1, \ldots, n.$$

In vector notation, (1) becomes

$$dx/dt = f[x(t), u(t)]$$

where $x(t)$ is an $n \times 1$ vector, representing the state of the system (e.g. species density), $u(t)$ is an $r \times 1$ input or control vector (e.g. harvest quota or harvest rate), and f is a vector-valued function. With time delays T, we have

$$(2)\quad dx(t)/dt = f[x(t-T), u(t-T)],$$

and for discrete systems,

$$(3)\quad x(k+1) = f[x(k), u(k)]$$

where k is the kth time interval.

The optimal control problem is stated as follows: Given the state eq. (1), a set of boundary conditions on the state variables at the initial and terminal times, and a set of constraints on the state and control variables, determine the admissible controls $u(t)$ so that a performance index (cost function) is minimized (or maximized). The boundary conditions are given by $x(t_0)$ and $S[x(t_f)]$ where t_0, t_f, and S denote, respectively, the initial time, the final time, and the target set. Note that t_0 is always fixed, but t_f may be part of the optimal control problem; e.g. one may strive to minimize t_f.

The performance index is expressed as a scalar quantity

$$(4)\quad I = G[x(t_f), t_f] + \int_{t_0}^{t_f} F[x(t), u(t), t]dt$$

where G and F are scalar-valued functions.

The main theoretical approaches to the optimal-control-

[1]Contribution No. 169 of the University of Minnesota Sea Grant College Program.

[2]Contribution No. 14696 of the University of Minnesota Agricultural Experiment Station.

system design utilize calculus of variation (Luenberger 1969; Clark 1976a), the maximum principle (Pontryagin et al. 1962; Athans and Falb 1966), dynamic programming (Bellman 1957; Larson 1968; Walters 1975; Walters and Hilborn 1976), and mathematical programming (Canon et al. 1970; Tabak and Kuo 1971). But for the simplest problems, analytical solutions by calculus of variation are unobtainable, and numerical solutions are considered most difficult.

The maximum principle, like the calculus of variation, leads to both analytical and numerical difficulties. Dynamic programming is an attractive alternative (Walters 1975; Walters and Hilborn 1976), but requires excessive computer memory (Bellman 1957; Larson 1968) and is applicable to small systems, with few variables only. Because of the ease with which mathematical programming deals with inequality constraints and small computer memory requirements, it is perhaps the most attractive method of solving optimal control problems, especially those that are nonlinear and which involve large systems. Yet, this method presents difficulties when nonlinear nonconvex functions are involved (Tabak and Kuo 1971). It also suffers from disadvantages similar to simulations in that general conclusions are often difficult to derive and problem solutions are specific.

Single-Species Models

The theory of optimal harvesting of single-species populations is well developed, and solutions exist for models such as the logistic (Goh 1969–70; Clark 1973; Cliff and Vincent 1973; Gopalsamy 1980), the stock–recruitment model for nonoverlapping generations (Moran 1950; Ricker 1954; Hassell 1975; Goh and Agnew 1978), the Beverton–Holt model (Beverton and Holt 1957), fisheries with limited season (Clark 1976a; Goh 1980a), and fisheries with delayed recruitment (Clark 1976b).

Continuous Models

Essentially, all continuous single-species models are of the form (1) or (2). When the control variable is linear in the objective function and the system dynamics, as may happen in many ecological control problems (Goh 1969–70; Cliff and Vincent 1973; Goh et al. 1974; Clark 1976a; Wickwire 1977; Clark et al. 1979), the optimal control solution is either bang-bang or singular. Bang-bang control refers to an optimal solution which dictates that the control switches between two values only: its maximum or its minimum. Singular control arises when the optimization criterion equals zero (for further details refer, for example, to Lee and Markus 1967; Clark 1976a). Using the generalized Legendre conditions, Goh (1966a, 1966b) derived the set of necessary conditions for singular control, which was also discussed by Clark (1976a).

Optimal control solutions usually consider a planning time horizon which might be finite or infinite. To test for long-term optimality, the focal point condition must be satisfied (Bliss 1946; Goh 1966a). When optimizing with the time horizon infinite, the integral objective function (4) becomes infinite. To overcome this problem, (1) a discount factor may be introduced (Clark 1976a), (2) the problem may be tentatively considered on finite time horizon and then the terminal time is shifted to infinity (Goh 1969–70), or (3) an average cost function may be minimized (Vincent et al. 1977).

For example, when a fish population of density N is harvested at a rate u, the logistic model of the exploited population is

$$(5) \quad dN/dt = rN(K - N)/K - u$$

where r and K are positive constants. To maximize the average yield from the fishery during the period $[0, T]$, T unconstrained, minimize

$$J = -\frac{1}{T}\int_0^T u dt.$$

The steady-state solution, with T unbounded, p denoting the costate and an asterisk denoting the optimal solution, is $N^* = K/2, p^* = 1, u^* = rK/4$ (Goh 1980a).

For a finite time horizon, the optimal control u, $0 \leq u(t) \leq u_{max}$ for the objective

$$\max J = \int_0^T u(t)dt$$

given (5) and $N(T) > 0$ is as follows (Goh 1980a): If $u_{max} > rK/4$, then the controls can switch among $u(t) = u_{max}$, $u(t) = 0$, or the singular control $u(t) = rK/4$, depending on time and the initial population density. If $u_{max} < rK/4$, then the optimal policy can lead to stable or unstable population density, depending on the initial conditions. When u is replaced with EN in (5), where E denotes the effort, then the optimal policy results in global equilibrium (Cliff and Vincent 1973). Thus, for a population which behaves according to the logistic model, regulation of the fisheries by effort, as opposed to quota, would result in a more stable fishery.

Optimal size limit for the Beverton and Holt (1957) model was derived by Goh (1980a). The solution depends primarily on the fish growth function and natural mortality. This is an important case, for: (1) regulating optimal size could be accomplished by mesh size regulation and (2) the approach is applicable to populations with highly variable recruitment.

Discrete Models

Formulating optimal control problems in discrete time has several advantages: many populations reproduce at discrete time intervals, and some even have nonoverlapping generations; population manipulations are usually seasonal, and can be represented by discrete events; many natural populations incorporate time lags in their dynamics, which present difficulties in continuous time optimization problems; algorithms to solve optimal control problems are discrete; mathematical programming and discrete time optimal control problems are similar (Canon et al. 1970; Tabak and Kuo 1971); singular control problems pose little difficulty in the discrete case; and abnormality (the case where there are too many constraints) can be dealt with by telescoping two or more time units (Goh 1980a).

Disadvantages of discrete time models are the theory on finite region of attraction and global stability is limited (Kalman and Bertram 1960; Diamond 1976; LaSalle 1976; Goh 1977; Fisher and Goh 1977), it is difficult to construct Liapunov functions for such models, and models with differential equations are usually more revealing and less complex for populations with overlapping generations (Nisbet and Gurney 1982). The relationships between delay differential equations and difference equations were explored by Blythe et al. (1982).

A general class of discrete time optimal control problems is the model

$$(6) \quad N(t + 1) = N(t)F[N(t)] - u(t + 1)$$

where $N(t)$ denotes the post-harvest population density with discrete and nonoverlapping generations, $u(t)$ denotes the number harvested at time t, the duration of harvesting is brief and

occurs before spawning, F is some recruitment function (e.g. Ricker 1954), and $t = 0, 1, 2, \ldots, T - 1$. To maximize the total yield during the period $[1, T]$, and for steady state, we need to solve the equation

$$1 = d[N(t)F(N(t))]/dN(t)$$

for N^* and apply the solution to (6). This in turn will result in optimal u^* which is also the maximum sustainable yield (MSY). The optimal control of this problem was derived by Goh (1980a), who also showed that when the harvest policy is constant quota, the MSY is unstable; when the policy is constant fraction, the MSY is locally stable.

Another important and general case of optimal control problem arises when it takes several years for an individual to reach sexual maturity (e.g. whales). The difference equation with time delays is (Clark 1976b) then

$$N(t + 1) = [1 - E(t + 1)][(sN(t) + F(N(t - 1))]$$

where $E(t + 1)$ is the fraction of the population which is harvested impulsively just before reproduction takes place, s is the fraction of adults that survive during the interval $[t, t + 1]$ in the absence of harvesting and $F(N(t - 1))$ is the recruitment to the adult population at time $t + 1$ which is due to the reproducing population at times $t - 1$. Clark (1976b) and Goh (1980a) derived the steady-state optimal solution (which maximizes yield) for this problem.

An interesting case arises when the *finite* mortality due to natural causes and due to harvesting interact (the so-called compensatory mortality). This case is important in applications, for often it is impossible to empirically establish the instantaneous rates whereas determining the finite rates of mortality is feasible (Anderson and Burnham 1975). In that case, the harvest may increase, but not without bound. Furthermore, the allowed harvest is more sensitive to changes in the amount of compensation than to changes in the finite mortality (Cohen 1986).

Multispecies Models

Current Models

Optimal control of more than two-species ecosystems poses a major difficulty, and many of the results of optimal control theory apply to two species only. Goh (1980a) proved that for two competing species with the Lotka–Voltera model, local stability implies global stability. For more than two competing species this result is not necessarily true. For any finite number of species, the Lotka–Voltera model of mutualism is globally stable if it is locally stable (Goh 1979). In a way similar to the graphical analysis of two-species interactions (MacArthur 1963), Goh (1980a) demonstrated that the nonlinear model

$$(7) \quad \begin{aligned} dN_1/dt &= N_1F_1(N_1, N_2) \\ dN_2/dt &= N_2F_2(N_1, N_2) \end{aligned}$$

is globally stable if (1) there is a positive equilibrium, (2) both species are self-regulating at all densities, and (3) the combined intraspecific interaction is stronger than the interspecific interactions. This is a general result, for not only is the nonlinear model (7) implicit, but the nature of interspecific interactions (e.g. predator–prey, competition, mutualism) is not specified. The system (7) remains globally stable under constant-effort harvesting policy.

For the general discrete nonlinear system model

$$N_i(t + 1) = G_i(N_1, N_2, \ldots, N_m)$$

where $i = 1, 2, \ldots, m$, Goh (1980a) derived a Liapunov function and the set of sufficient conditions for global stability.

For systems with more than two species, the optimal harvesting theory is not as well developed as for two species. Because of the added complexity, many authors (e.g. Goh 1980a; Vincent 1980) discuss only simplified mathematical models of multispecies communities. For example, a model which was analyzed extensively by Clark (1976a) includes economic as well as biological considerations, and thus renders the analysis of management options more realistic. Let

$$dN_i/dt = G_i(N) - u_i, i = 1, 2, \ldots, m$$

for the planning period $[0, T]$. Also, let $N_i(T) \geq e_i$, $i = 1, 2, \ldots, m$, where e_i is a positive constant, which is chosen such that the community remains viable after time T. Furthermore, the harvest rates are bounded from above such that

$$b_i \geq u_i(t) \geq 0, i = 1, 2, \ldots, m$$

where b_i is constant ($i = 1, 2, \ldots, m$). The problem is to choose the functions $u_i(t)$ which will drive the system from the initial state $N_i(0)$ so as to maximize the present value integral

$$J = \int_0^T e^{-\delta t}\left[\sum_{i=1}^{m} (v_i - c_i/N_i)u_i\right]dt$$

where v_i is the price for fish of the ith species, c_iu_i/N_i is the cost of harvesting the ith species at the rate of u_i, and δ is the discount rate. Thus, we are trying to maximize the discounted net revenue (Clark 1976a; Silver and Smith 1977). The analysis of single-species models, which was not confirmed for multispecies models, suggests three stages of harvesting: (1) bring the community to a desired level as soon as possible (by allowing maximal or minimal harvest); (2) keep the community at the specified constant level until just before the end of the planning period; and (3) bring the community to the terminal state, which is specified in the problem.

Extensions to Existing Models

Little is known about the optimal fishery policy of age–size-specific models. The importance of age structure in ecological models was reviewed by Oster (1978) and Hassell (1978). Recently, Hastings and Wollkind (1982) proposed a modelling technique which allows determination of the magnitude of the effect of age structure on stability. Some authors advocate inclusion of information regarding individuals into models. For example, Botsford (1980) demonstrated that a narrow, peaked influence of older animals on recruitment over age is less stable than a broad, flat influence. Thus, the earlier conjecture that fishing stabilizes populations is not supported in all cases. This is so because age- or size-selective fishing removes animals of older ages, which narrows the influence over age of older animals on recruitment and can make the population unstable. Another interesting result is provided by the discrete time and age model of the Ricker stock–recruitment relationship. Levin and Goodyear (1980) showed that as mortality rate of older individuals is increased, it first increases and then decreases population stability, and even fishing that is not age or size selective can make a population less stable.

The traditional way of dealing with optimal harvest policy of age- or size-specific models has been restricted largely to the Leslie matrix model. Since the model is linear, harvesting is permitted only when eigenvalues are greater than 1, and optimal fishing dictates harvesting only towards the end of the planning

period. Thus, some authors (e.g. Beddington and Taylor 1973; Rorres and Fair 1975; Rorres 1976; Mendelssohn 1976) believe that these models are of limited value.

A more realistic application of the Leslie matrix model includes stochastic fluctuations in fish populations. Numerical studies of the Leslie matrix which include stochastic fluctuations in one or more age-specific vital rates were conducted by Allen and Basasibwaki (1974), Jensen (1975), Vaughan (1977), Boyce (1977, 1979), DeAngelis et al. (1977), Deriso (1980), Christensen et al. (1982), Slade and Levenson (1982), and Ginzburg et al. (1983). More general analytical approaches of these models were studied by Cohen (1977a, 1977b, 1979a, 1979b, 1979c, 1980), Lange (1979), Lange and Hargrove (1980), Lange and Holmes (1981), and Tuljapurkar and Orzack (1980). Cohen et al. (1983) computed both the point and interval estimates of the growth rate of the average population size of the striped bass (*Morone saxatilis*). Sykes (1969) and Pollard (1966, 1973) analyzed stochastic versions of the Leslie matrix and concluded that considering the transition matrices as random variables provided a satisfactory model for estimating variances of population numbers.

It seems that when individual age–size-specific considerations are included in traditional harvesting models (e.g. logistic), the optimal harvest policy is different. For example, Botsford (1980) hypothesized that when multiple age classes with density-dependent growth and recruitment rates are included in the logistic growth model, the optimal harvesting might be pulse fishing rather than constant fishing. Similar conjecture was advanced by Clark (1976a) for models which include constant-recruitment, multiple age class. Similarly, in simulation experiments, Hannesson (1975) concluded that pulse fishing is better than stationary fishing when fishing costs are not zero. Walters (1969) obtained (numerically) the MSY dictated by models which include individual growth and stock–recruitment relationships. For the case of no fishing selectivity, he concluded that pulse fishing was optimal. When fishing selectivity was included in the model, constant harvesting policy was optimal. A similar model, with no gear selectivity, dictates pulse fishing as the optimal harvesting policy (Pope 1973).

Thus, the differences in the results of optimal harvesting policies between population models which do and do not include age- or size-specific considerations at the individual level indicate that more detailed models should be analyzed. On the other hand, inclusion of individual characteristics in multispecies models results in excessively complex models, which are difficult to deal with even with simulations. Furthermore, including age structure in single-species models usually changes the quantitative aspect of the models, but seldom affects their dynamic behavior (Nisbet and Gurney 1982). Blythe et al. (1982) argued that much of the burden of analyzing models which include age structure can be overcome by using delay-differential equations where the time lag accounts for the maturation period.

Another aspect of age-specific models is the assumption of stable age distribution (Fisher 1930; Thompson and Bell 1934; Cole 1954; Beverton and Holt 1957). The implications of relaxing this assumption have not been studied extensively (Stearns 1976), and as Sinclair et al. (1983) reported, relaxing the assumption of stable age distribution for population models of different fish species has different impacts on population production, depending on the different growth rate at different ages of various species. Thus, deviations from stable age distributions for Atlantic mackerel (*Scomber scrombus*) would have a greater impact on population production than would a similar deviation for Atlantic cod (*Gadus morhua*) (Sinclair et al. 1983).

The simplifying assumption that individuals spawn once, and at a common age, which is central to many stock–recruitment models, may result in oversight (Levin 1980). This is especially true when reproduction is spread over several age classes, such as in the striped bass. The properties of models which include multiple-age spawning were investigated, among others, by Walters (1969), Allen and Basasibwaki (1974), and Levin (1980). Generally, with the inclusion of age-specific parameters, the behavior of even the simplest fisheries models becomes more complicated, and fishing might or might not stabilize the population.

Goh (1980b) argued that for species with high fecundity and large fluctuations in recruitment, deterministic stock–recruitment models should be abandoned, and the return from using realistic stochastic models does not justify the modelling effort. Furthermore, the concept of MSY is not valid, and the best policy is to provide a set of guidelines whose objective is to prevent the collapse of the fisheries. For optimal policy of maximum biomass, these guidelines dictate optimal size limit. This approach admits that there are no long-term dynamics of the fish population. On the other hand, for species with low fecundity (e.g. whales), and when the population is large, one may use deterministic population models, and the tools of optimal control theory may be applied to derive optimal harvesting policy. This is so because the relationships between fecundity and the parent stock are well defined.

Much of both control of and inputs to ecosystems are periodic. Therefore, the topic of linear periodic control may provide some further insights into optimal control problems. This is particularly true, since the solution of the linear control problem

$$dx/dt = A(t)x + u(t),$$

where both the matrix $A(t)$ and the control vector $u(t)$ are periodic, does not in general exhibit periodic behavior of $x(t)$. Emanuel and Mulholland (1976) applied linear periodic control and derived an optimal fertilizing schedule for a sport fishing pond which should result in increased productivity.

Stability

One objective of fisheries management may be to produce a stable and reliable resource, in which case stability analysis becomes important. The general model to be considered is

$$(8) \quad dN_i/dt = N_i F_i(N_1, N_2, \ldots, N_m)$$

where $F_i(N)$ are continuous functions in the positive orthant. Stability may be divided into local and global, and the distinction between them is important.

Local Stability

An ecosystem model is locally stable if every trajectory of the model which begins in the neighborhood of a particular equilibrium point remains in it for all values of time t and converges to that equilibrium point as $t \rightarrow \infty$.

When model parameters are known, local stability may be studied by linearizing (8) and applying eigenvalue analysis (May 1974). When the ecosystem model is not large (e.g. $m < 5$), and when the parameters of F in (8) are not known, the Routh–Hurwitz stability criterion may be used to establish

conditions for local stability. Another criterion which may be used to establish necessary and sufficient conditions for local stability is that of Willems (1970).

Using linear or linearized models has several advantages: the theory of linear systems is well developed, analytical solutions exist in many cases, and the optimal feedback control law for stochastic and deterministic models is the same for the general linear regulator problem (Fleming and Rishel 1975). Linear models are not totally useless, especially when the ecosystem is managed in the neighborhood of some well-defined operating point. Some authors (Nisbet and Gurney 1982) claim that examination of local stability by linearizing model equations provides much insight into the global stability of nonlinear models.

Global Stability

An ecosystem model is globally stable if every trajectory of the state variables which begins in the positive orthant remains in it for all values of time t and converges to a positive equilibrium as $t \to \infty$. Most fisheries models are nonlinear, and global stability analysis is often necessary. Global stability may be examined with the use of Liapunov functions (Liapunov 1966; Barbashin 1970; LaSalle 1976). Goh (1980a) proposed the use of two-sided energy principle in conjunction with the direct method of Liapunov. Two-sided energy principle is needed because unlike physical systems, viable populations must absorb energy at low densities and dissipate energy at high densities. Goh (1980a) derived the finite region of stability for model (8) and showed that global stability does not exist for a single species with model (8) and constant quota harvesting.

Specifically, a Liapunov function of the single-species model

$$(9) \quad dN/dt = NF(N)$$

with a positive equilibrium N^* is

$$V(N) = N - N^* - N^* \ln (N/N^*).$$

Model (9) is globally stable if $N^* > N > 0$ implies $F(N) > 0$ and if $N > N^*$ implies $F(N) < 0$ (Goh 1980a).

A multispecies system of the form

$$(10) \quad dN_i/dt = N_iF_i(N_1, N_2, \ldots, N_m)$$

is globally stable if (1) the equilibrium N_i^* $(i = 1, 2, \ldots, m)$ is in the positive orthant and (2) the interspecific interactions are weak relative to the self-regulating intraspecific interactions. For a rigorous proof, see Goh (1980a, p. 192).

As opposed to constant effort, constant quota harvesting usually results in unstable population size (Goh 1969–70; Beddington and May 1977). This is especially true when the harvesting technology is very efficient. For example, consider the single-species population exploitation model

$$(11) \quad dN/dt = NF(N) - EN$$

where E is a measure of the amount of effort applied in harvesting the popultion. If $F(N)$ is strictly monotonic decreasing as N increases, and if N has positive equilibria for both the exploited and unexploited population, then the population has global equilibria in both cases (Goh 1980a).

The above result is rather general and applies to many single-species models (e.g. Gilpin and Ayala 1973; Schoener 1973). If the population sustains an Allee effect (where a threshold population size below which the population cannot sustain itself exists; Pianka 1972), then the population model with and without harvesting may be qualitatively different.

Goh (1980a) extended model (11) to the case when both handling time of the harvested resource and competition among harvesters are considered. He then derived the conditions for stability of a general class of single-species harvesting models for $F(N)$ as in (11). Based on the results of stability analysis, it seems that regulation on the basis of effort rather than quota should be implemented wherever possible. However, as opposed to catch quotas, which are easier to monitor and apply, fishing effort is notoriously difficult to measure and quantify (Butterworth and Newman 1980).

The difficulties with analyzing global stability of ecosystems by the Liapunov or Liapunov-like method are as follows: (1) Although the literature on the construction of Liapunov functions is extensive (Schultz 1965; Hahn 1967; Gurel and Lapidus 1968, 1969; Willems 1970; Gilpin 1974; Gatto and Rinaldi 1977; Goh 1977; Hsu 1978; Goh 1980a), constructing a Liapunov function is not a trivial task, and there is no guaranteed method of finding a Liapunov function for general nonlinear systems. Hsu (1978) and Goh (1980a) have established Liapunov functions for a number of population models, and Ingwerson (1961) and Zubov (1964) proposed methods of establishing Liapunov functions for some classes of nonlinear models. (2) Since the conditions for global stability are sufficient, one has to assume that equilibrium exists before applying these methods. (3) An infinite time interval is used when a finite time interval is more useful in practice. (4) Because of the way Liapunov functions are defined, the system could be stable according to the definition, but not from a practical point of view. Nisbet and Gurney (1982) argued that the usefulness of Liapunov method for establishing global stability in ecological systems is limited.

The concept of stability is of limited value, for it establishes global stability relative to realistic perturbations from initial conditions. Most ecosystems are subject to continuous disturbance, and the concept of vulnerability is thus more useful.

Vulnerability

The concept of nonvulnerability, which describes the system ability to withstand unpredictable, large, and continual disturbances, is of much practical importance (LaSalle and Lefschetz 1961; Lashiher and Storey 1972; Goh 1975, 1976; Holling 1973; Harrison 1979; Vincent and Anderson 1979; Vincent and Skowronski 1980). This concept, which is closely related to the ideas of reachability and controllability in control systems theory (e.g. Lee and Markus 1967), was developed by Goh (1975, 1976) and Grantham and Vincent (1975).

Consider an ecosystem model during the time interval $[0, T]$. Define $S(0)$ as a set of desirable states and $Z(T)$ the set of undesirable states. Let $u_i(t)$ $(i = 1, 2, \ldots, n)$ be a class of continual disturbances where $u_L \leq u_i \leq u_M$ and where u_i is piecewise continuous.

The system

$$dN_i/dt = N_iF_i(N_1, N_2, \ldots, N_m; u_1, u_2, \ldots, u_n)$$

is vulnerable during $[0, T]$ if there exists an admissible set of functions $u_1(t)$, $u_2(t)$, $\ldots$, $u_n(t)$ which could drive the system from $S(0)$ to $Z(T)$. Otherwise the system is nonvulnerable (Goh 1980a). Vincent and Anderson (1979) have modified the above definition and analyzed vulnerability in a more qualitative way. Accordingly, they define system A to be more vulnerable than system B if any species in system A can be driven more closely to extinction than any species in system B under the disturbing function.

Vulnerability can be analyzed with the help of Liapunov-like functions, where sufficient conditions for nonvulnerability can be examined for $[0, T]$ and $[0, \infty]$. One difficulty with this method is the numerical establishment of global maximum of a function of many variables. Another approach to the study of nonvulnerability is to set up the model ecosystem as an optimal control problem and to specify the worst possible combination of the control variables (=disturbances). The analysis in this case is very conservative.

Using the technique of Liapunov-like functions, Goh (1980a) derived the necessary conditions for nonvulnerability of a species whose population behaves according to the logistic model and who is subjected to predation by a very efficient self-regulating predator. As in the continuous case, Goh (1980a) derived the set of sufficient conditions for the existence of nonvulnerability of the system

$$N_i(t+1) = F_i(N_1, N_2, \ldots, N_m; u_1, u_2, \ldots, u_n)$$

during the interval $[0, T]$ and $[0, \infty]$.

Using a predator–prey model with known continuous disturbance and with particular parameter values, Fisher and Goh (1980) proved that when optimal harvesting of both species is added to the system, it becomes less vulnerable in the sense that species populations are less likely to become too low; e.g. the species populations will not drop to a level below 15% of their equilibrium. Similar results were obtained for the Lotka–Voltera competition model with particular parameter values and with harvesting of only one species; i.e. the system becomes less vulnerable. The generality of these results remains to be seen.

Using the simple predator–prey model with harvesting for the baleen whale – krill system (May et al. 1979), Vincent (1980) introduced the concept of the Nash solution. For each level of sustained harvest, there is an equilibrium solution. The Nash solution is that where the sustained yield level from the system cannot be increased by increasing the effort of one harvester without affecting the harvest by other harvesters. The whale–krill model is stable under effort harvesting, and none of the species will be driven to extinction using Nash limits on the harvesting efforts. The difficulties with this approach are (1) it is assumed that none of the species is endangered at the Nash equilibrium point, (2) the prey population can be driven to a level lower than the Nash equilibrium, and thus become endangered, and (3) unless one considers a system whose major dynamics are truly dominated by two species only, there is a need to include more components in the system.

The relationships between vulnerability and return time (to equilibrium) were investigated by Vincent and Anderson (1979). It follows that when trophic levels are added to model ecosystems, the return time increases, but vulnerability may decrease. The vulnerability analysis is also useful in management under uncertainty, and optimal controller which drives the system under uncertain disturbance back to stable equilibrium was derived (Vincent 1987).

Prospects and Problems

This section lists some of the current problems and possible extensions of modelling fisheries systems.

Modelling with distributed parameter systems holds much promise. This is true because (1) modelling age and size class distributions reveals unexpected population dynamics (e.g. Botsford 1980; Levin 1980), (2) for many fish species, density distribution has strong temporal and spatial components, and (3) recently there has been much interest in biomass spectrum. Partial differential equations for some classes of age-structured populations were derived by Ahlgren (1981), Nisbet and Gurney (1982), and others. Optimal control theory of distributed parameter systems is treated in Sage (1968), Butkowskiy (1969), and Lions (1971). I am unaware of applications of distributed control systems to fisheries management.

One of the most difficult problems is to ascertain that models truly represent essential dynamics of systems. For example, vulnerability analysis with the concept of Nash equilibrium (Vincent 1980) assumes that the predator–prey model of the baleen whale – krill system (May et al. 1979) is correct. This then relates to the problem of local and global identifiability of models (Walter 1982); i.e. to what extent is a model unique in describing the relationships between inputs and outputs? Is it possible to propose other models that would give the same outputs from the same inputs? The identifiability problem is especially acute when model forecasts are used as guidelines for management decisions, when parameter estimation is crucial, and when models are used as aids for experimental design. Little attention is given to model identification in the ecological literature. This important topic is well treated by Bekey (1970), Banks (1980), Walter (1982), and others, who derived necessary conditions for local and global identifiability of state space models.

The difficulty of numerical solutions of dynamic optimal models is well recognized (Bekey 1970; Goh 1980a). Thus, it is recommended to use various algorithms with as many initial conditions as possible in solving optimal control problems (e.g. Fletcher 1975). The cost of such procedures can become prohibitive very quickly.

How can we justify ignoring certain forces within the ecosystem and claim that their consequences are negligible? It seems that often, biological mechanisms are not incorporated into mathematical models simply because they result in models which are too complicated. For example, Botsford (1980) and Sinclair et al. (1983) have demonstrated the importance of including age or size structure in fisheries models whereas Nisbet and Gurney (1982) discounted the importance of age structure in single-species population models. This problem is further compounded by the fact that when age structure is incorporated into mathematical models, they become quickly untractable, unless some questionable simplifying assumptions are adopted (e.g. see reviews by Hassell 1978; Oster 1978).

Most of the difficulties in modelling arise while building models, rather than during their analysis. For these kind of problems, little formalism exists (but see Ziegler 1976) and biological as well as mathematical sophistication is essential. Unfortunately, most scientists are competent at either one but not both subjects.

The existing fishery models all fall short of complete realistic description of population dynamics (Botsford 1980), and much effort should be invested in interpreting the biological meaning of model parameters. A lucid example was provided by Iwasa and Roughgarden (1984), who were able to interpret the biological significance of the costate variables in an optimal control problem of allocating growth to shoot/root versus reproductive tissue in plants.

Environmental conditions play an important role in determining year-class strength, and stock size may play a secondary role only (Sissenwine 1977; Van Winkle et al. 1979; Left and Kohler 1976; Nelson et al. 1976; Swartzman et al. 1983). Therefore,

future models will have to include more environmental driving variables directly. These might enable us to account for some of the tremendous variability in recruitment. Thus, coordination of environmental and fisheries biology research should be encouraged (Butterworth and Newman 1980). In that respect, studies such as those of Swartzman et al. (1983), where age structure and ambient temperature were incorporated into a population model of the Pacific whiting (*Merluccius productus*), or Pauly (1980), who studied the relationship between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks, should be welcomed.

Incorporating economic considerations in biological models will result not only in more realistic models, but also in management objectives which might be achievable. For example, Botsford et al. (1983) demonstrated that harvest rate responds (with a lag) to fluctuations in the population of the Dungeness crab (*Cancer magister*) off the coast of California and that this lagged response is a potential cause of the population cycles. Thus, it seems that understanding the link between fluctuations in effort and fluctuations in fish populations may result in management policies which may be realistically achievable. For example, if delayed response in effort (due to market and other characteristics) contributes to population fluctuations, we may seek policies which will reduce the lag period.

Most of the modelling efforts in fisheries have concentrated on models which include biological mechanisms. Purely statistical approaches are limited (e.g. Mendelssohn 1980; Saila et al. 1980; Roff 1983), but still hold promise (e.g. Cohen et al. 1987), at least in terms of their ability to forecast (e.g. Cohen and Stone 1987). It seems that until the many problems in the mechanistic models are solved, and since policy decisions are undertaken continuously, there is room for more pragmatic models such as time series analysis (Box and Jenkins 1976).

One of the most difficult problems is to communicate the results of modelling efforts to the user (e.g. fisheries managers). This is particularly important, for many of the models in fisheries can be judged solely by their ability to help in managing the resource. A lucid review of one success story, where a model was devised, communicated, and successfully implemented, is given in Hilborn et al. (1984). Perhaps modellers need to develop a model of how models can be communicated, applied, and tested. Adaptive management (Walters 1986) is particularly useful in this respect.

It seems that the concept of MSY is not as useful as might appear from the number of publications that are dedicated to analyzing it. Furthermore, the distinction between strategic and tactic models (Nisbet and Gurney 1982) should be recognized as a continuum; both have a place in management applications. All of the applications reviewed herein are based on analytical models. They are, in most cases, limited to analysis of general models, rather than solutions of specific management problems. Other aspects of control theory, such as dynamic programming (Bellman and Kalaba 1965), are more useful for specific problems. Finally, game theory (e.g. Friedman 1971; Vincent and Gayeck 1982; Vincent and Brown 1984) will probably prove useful in future research of harvest theory and perhaps applications.

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Ecological Stability in the Context of Multispecies Fisheries

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Recent theoretical studies suggest that disrupted communities are not persistent in the face of attempted invasions; moreover, reassembly of a persistent community is likely to prove difficult. It appears that the most likely species to invade a harvested community are those most similar to the harvested species, except in their propensity to be harvested. Most communities are not resistant to removals of top predators; large changes in species composition usually ensue. Large changes in community composition may, however, be associated with small changes in total biomass. Although there is some debate over whether natural communities are, on average, resistant, given species additions, community changes following species introductions appear to be common, especially in harvested or polluted systems where man effects a positive feedback between extinctions and invasions. There are several alternative theoretical relationships between population resilience, variability, and stress; the choices strongly depend on the underlying mathematical model. Multispecies models suggest that the relationship will depend on the relation of the population to other species. Empirical analyses have been highly deficient, primarily because of the failure to distinguish different temporal scales of variability.

Selon de récentes études théoriques, les communautés perturtbées ne résistent pas aux tentatives d'invasion; de plus, le rassemblement d'une communauté résistante sera probablement difficile. Il semble que les espèces les plus susceptibles d'envahir une communauté exploitée soient celles qui ressemblent le plus aux espèces exploitées sauf pour ce qui est de leur penchant à être capturées. La plupart des communautés ne résistent pas à la disparition des principaux prédateurs qui est suivie d'importantes modifications de la composition spécifique. Celles-ci peuvent toutefois être associées à de petites variations de la biomasse totale. Quoiqu'il existe une certaine controverse quant à la résistance de communautés naturelles à la suite de l'apport de nouvelles espèces, des modifications de la structure communautaire après de tels apports semblent être communes surtout dans les systèmes exploités ou pollués où l'homme apporte une rétroaction positive entre les invasions et les disparitions. Il existe plusieurs autres relations théoriques entre la résistance d'une population, la variabilité et le stress; les choix dépendent fortement du modèle mathématique sous-jacent. Selon des modéles multispécifiques, le rapport dépend de la relation entre la population et les autres espèces. Des analyses empiriques ont donné très peu de résultats, surtout à cause de l'impossibilité de distinguer entre les différentes échelles temporelles de variabilité.

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Single-species models are inadequate for solving many applied ecological problems. It is clear that model parameters are themselves variable, due, in part, to their dependence on the species' interactions with other species in the community. In trying to understand these interrelationships, ecologists have taken a variety of approaches.

Simulation modellers (e.g. N. Bax and T. Laevastu, unpubl. data) encapsulate what is known about the community in equations much too complicated to be understood analytically and thus they run numerical experiments on the computer. More empirically minded ecologists may try to find where the strongest interactions are between species, in order to reduce the complexity of the problem. Many papers in this issue take this approach and a summary of these interactions from the Great Lakes is provided by Crowder et al. (1987). Even here, the complexity of the problem is apparent. The number of interactions is large enough that we can do little but look at the entire synthesis as some abstract work of art, while examining the few interactions we know personally and noting how crudely the table portrays their underlying complex reality.

We seek additional methods for understanding multispecies dynamics. We deliberately say "additional" and not "alternative" because the diversity of problems facing ecologists strongly argues for pluralism. Rather than concentrating on each upward or downward movement of a population, discussions of ecological stability seek descriptions of population and community dynamics that capture the principal features of observed changes. If we can catalogue these features, we may be able to ask what causes them, in terms of biological variables we know or can measure. These characterizations will necessitate a multispecies perspective, the population and community simply being different levels at which we observe the effects of species

interactions. We are sacrificing detail for generalities about multispecies dynamics which, if they exist, we may have some hope of understanding.

A simple example is in order. Figure 1 shows the Michigan landings of lake trout (*Salvelinus namaycush*) in Lake Superior. The changes in this fishery are complex, but we would argue that these data suggest a limited number of features for consideration. By fitting a moving average to these data, we can look for a long-term *trend*. There is a pronounced decrease around 1950; this is when the sea lamprey (*Petromyzon marinus*) invaded the community. There is some residual variation about this long-term trend. It is not without pattern, for, as can be seen, there is an obvious cyclical pattern in the landings. We can factor out this *cycle* using statistical procedures, leaving behind short-term (i.e. year-to-year) variation which we call *noise*.

"Trends," "cycles" and "noise" are, of course, three arbitrary points along a continuum of frequencies. One approach might be to characterize these data entirely by a plot of the amplitude against frequency. We then might classify the resultant plots into a number of distinct patterns and seek causes for these patterns. But whatever the formal procedures for analysing these data, we must still ask: what factors cause these changes in landings at such very different time scales?

The questions we seek to ask in this paper all follow immediately from the preceding discussion. Can we understand why species have invaded the Great Lakes? Here we use the term invade to mean the successful establishment of an exotic species. Also, are some communities more *persistent* than others, in that they admit fewer invaders? Given an invasion, how much of an impact on the abundances of individual native species should the invader have? And how much impact will there be on the total biomass of species? That is, in terms of composition or total biomass, are some communities more *resistant* than others? What factors predispose populations to cycle and how *variable* should densities be about their long-term trend? And are some populations more *resilient* than others, in that they return more quickly to this long-term trend?

Before we begin to examine these questions, we want briefly to examine the meanings of the word stability. The preceding terms are often those meant when we use the term stability loosely. Elsewhere (Pimm 1984a) we have argued that resilience, persistence, resistance, and variability may be more interesting to ecologists than the strict mathematical definition of stability. A community is deemed stable if and only if all the population densities return to equilibrium following a perturbation. This is easy to determine for model communities — at least for densities close to equilibrium — and there is a considerable literature on its application in ecological models. We have reviewed elsewhere what this literature might mean (Pimm 1982, 1984a). Arguably, the results say little about comparisons of existing communities. Suppose we expect natural communities to have predominantly, although not exclusively, stable equilibria. Then studies of stability provide comparisons of extinct and extant communities, the former being the unstable communities that have long since disintegrated into stable configurations. This view of stability allows us to predict a wide range of food web patterns (Pimm 1982). But if we want to compare existing communities, we must look for other ways of describing multispecies dynamics.

Now we *can* ask whether one existing community is more persistent or resistant than another, or whether one population is more resilient or variable than another, and why. These terms

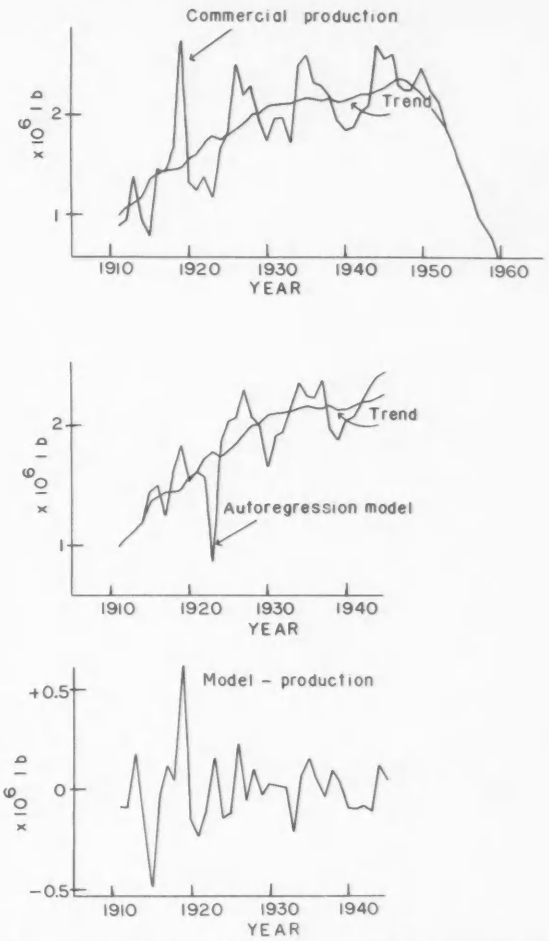

FIG. 1. Michigan landings of lake trout in Lake Superior. Shown here is one method to separate trends, cycles, and noise from time series data (see text). Top: landings (1911–59) fitted with a 9-yr moving average (trend). Middle: a one-parameter (lag = 4 yr) autoregression model was fitted to the relative deviations of landings from the trend (1911–45). Shown are the predicted values from the model added back onto the trend values, along with the original trend. Bottom: residuals of the autoregression model.

are as mathematically tractable as stability, if somewhat less familiar, and they are often measurable in the field. We would argue that they correspond closely to the needs of the applied ecologist.

Persistence: When do Communities Permit Invasions?

What are the Factors to Consider?

The Great Lakes ecosystems are obviously very different now than they were a century ago. In particular, three species (sea lamprey, rainbow smelt (*Osmerus mordax*), and alewife (*Alosa pseudoharengus*)) have dramatically altered the species composition of the lakes. Some of the invasions are serious, while others are arguably so: the alewife provide a food resource for introduced salmonids (Kitchell and Hewett 1987). Aquatic

ecosystems, however, can be impacted either much more than the Great Lakes (e.g. Lake Gatun, Panama (Zaret and Paine 1973)) or much less. Two examples of the latter are (1) the North Sea which has not admitted any new species of fish, despite the obvious potential of colonists to reach the area, carried in the ballast water of ships, and (2) the Pacific ocean off Hawaii where there has been only a 33% success rate for known introductions, compared with a 76% success rate for the inland, nonmarine habitats (Maciolek 1984).

The Great Lakes are geologically very recent. It is just possible that what we are seeing are the more recent colonists in a natural successional sequence that started after the retreat of the ice. We might expect the species composition of the lakes to change, albeit over a long time scale. Man, however, has reduced the barriers to colonization in a variety of ways, and so the rate of species invasions has probably increased too. What we need to know is whether further invasions will occur and what their likely effects will be. Are there any obvious gaps that should be filled by invaders or are we creating gaps in an otherwise relatively persistent community when we harvest species?

To examine these possibilities, we might see if the existing communities have smaller numbers of species than we would expect on the basis of, say, the familiar species–area curve. There are some parallels here to Diamond's (1975) studies of bird communities on islands. Islands recently defaunated by volcanoes or tsunamis have, not surprisingly, fewer species than one might expect for their size. The problem with this approach is obvious. There are only a few other lakes of anywhere near the same size as the Great Lakes on the same continent from which to draw the species–area curve. We would be extrapolating from much smaller lakes, with all the attendant problems of prediction far from the range of one's data. We are therefore unlikely to predict, with any degree of confidence, a persistent number of fish species for the lakes from species–area relationships.

What we might seek are ways of predicting invasions from a more detailed knowledge of community structure. Stauffer (1984) pointed out that certain species are missing from areas that are potentially habitable with regard to environmental conditions, even when the species have dispersed to these areas in numbers sufficient for invasion. Thus the failures, as well as the successes, may have community-level explanations. The intensity of competition and predation might be expected to strongly affect the chance of a species invading, and we shall discuss these first. Then we shall consider whether we reduce a community's persistence when we harvest some of its species.

Competition: Theoretical and Observational Studies

Among the first studies to consider community persistence were those stimulated by Hutchinson's (1959) suggestion that the morphological characters of species seemed to differ by constant ratios. There might be a "limiting similarity": species too similar morphologically and, by extension, ecologically, were predicted to compete too strongly and so hasten the local extinction of one of them. In contrast, communities with morphologically very distinct species should be invaded quite easily. Simply, competition should lead to morphological characters that are "patterned," by which is meant, by analogy to spatial distributions, that they are overdispersed rather than random or aggregated.

Several types of morphological characteristics, including body size and shape (Werner 1984) and the number and length of gill rakers (Crowder 1984), have potential importance to community organization in fishes. Gatz (1979) found evidence for nonrandom division of resources within stream-fish assemblages by analyzing 56 morphological features, both external and internal. An assumption in these types of studies, often untested, is that morphological differentiation indicates ecological differentiation.

That Hutchinson's paper has been the motivation behind much of animal community ecology in the last 25 yr is apparent from the papers in three recent volumes devoted to community ecology (Cody and Diamond 1975; Diamond and Case 1985a; Strong et al. 1984b). Early results seemed encouraging. Theoretical studies (MacArthur and Levins 1967; May and MacArthur 1972) suggested a tight limit on the allowable morphological similarity between species, and empiricists claimed widespread evidence for community pattern in overdispersed morphological characters.

Later theoretical studies, however, have shown just how complex the patterns of morphological differences could be, even in communities where competition is important (Turelli 1978; Roughgarden 1985). Most of the theories suggest that a community will be difficult to invade if the potential invader faces too many competitors; but how many is too many is going to depend on a wide variety of factors.

But what of the data that spawned these studies? As Hutchinson suggested, if communities are highly patterned, is it due to their rejecting those species that are too ecologically similar to fit in? If so, the existence and clarity of the patterns in the morphological characters of species may give us a good predictor of the community's persistence. Deciding whether the morphological characters of species are in fact overdispersed, however, requires the statistical prediction of the "ghosts": those species which have attempted to invade a community and failed because they were too similar to existing species. Not surprisingly, no one has a universally accepted recipe for ghost prediction, and the literature on what we can deduce about communities from their current composition involves a heated debate (Lewin 1983a, 1983b). Not only is valid evidence for limiting similarity difficult to obtain, but in fish assemblages in particular, evidence against limiting similarity is often found (Findley and Findley 1985; Grossman, in Moyle et al. 1986).

Certainly, there is good experimental evidence that some species compete (Schoener 1983 is a review; 10 of 164 cases involving fish) just as there is equally good evidence that many species do not (Strong et al. 1984a). But experimental demonstrations of competition between a few species do not tell us if competition is intensive and extensive enough to structure entire communities by applying a strict filter on community membership. Simply, studies of existing community patterns are unsure ways of understanding what factors affect community persistence. To predict whether a species can invade a community, and if not, why not, we must use an experimental approach. Interestingly, the literature on species introduced by man is rich in examples and implications for community theory.

Competition and Experiments: Direct Studies of Species Invasions

If the studies of existing community patterns have generated more heat than light, it has probably been due to the lack of a direct, experimental data base from which to investigate persistence. Recently, there have been several studies aimed at

asking community-level questions using compilations of data on deliberately introduced species. In many cases, these studies provide documentation on those species which failed, as well as those that succeeded, and so avoid the messy statistics of predicting these "ghosts."

Three compilations look at various species invading communities of different composition: Moulton and Pimm (1985) is a review of their studies of bird introductions to Hawaii (where more bird species have been introduced than anywhere else), Simberloff (1986) discussed earlier studies of Hall and Ehler (1979) and Ehler and Hall (1982) on insects introduced for the biological control of insect pests, and Crawley (1986) reviewed plant introductions to Britain.

The studies demonstrate clear taxonomic differences in our ability to detect the effects of competition. For insects, there appears to be no detectable effect of community composition on invasion success. But for Hawaiian birds, species-rich communities are harder to invade than species-poor ones and there is evidence for limiting similarity: a species is more likely to fail in the presence of morphologically similar species. Perhaps more importantly is that data on invasions permit particularly simple evaluations of a wide range of questions involving what species are likely to invade and what community characteristics permit them to do so (Diamond and Case 1985b).

Although the literature on both successful and unsuccessful introductions of exotic fishes is vast (Courtenay and Stauffer 1984), there do not appear to be broad attempts to contrast the successes and failures of a single species in light of community characteristics. Fraser (1978) reported that the failure of planted salmonids in Little Minnow Lake was due to competition for food with yellow perch (*Perca flavescens*), but suggested that in larger lakes with natural assemblages of predators the effect of yellow perch may be ameliorated. Evans and Loftus (1987) looked at a single species, the rainbow smelt, and its success or failure in penetrating a range of different communities. In their study, there were clear differences between those lakes penetrated by smelt and those that were not. The features that distinguish "smelt lakes" are not independent of each other, but the separate effects can be teased apart statistically, and such a study is planned (D.O. Evans, pers. comm.).

Predation

As with competition, there is abundant evidence that predators are capable of severely reducing species numbers or excluding species from habitats (e.g. Zaret 1980). Yet again, the question is whether we can evaluate the likely pressure exerted by predators on a potential invader in terms of easy-to-measure features of community structure.

If there seems to have been less controversy about the effects of predation (as compared with competition) in structuring communities, then this must surely be an illusion. Lawton and colleagues (Lawton and Strong 1981; Jeffries and Lawton 1984, 1985) have argued from the models of Williamson (1957) and Holt (1977) the importance of "predator-free space." Much as two species cannot share too many of their essential resources and be expected to coexist, so two coexisting species cannot share sets of predators that are too similar. Thus, increases in one of the two species will increase the density of the predators and decrease the other species, leading to "apparent competition" between two species that do not necessarily share resources. Potential community patterns such as overdispersed morphological characters of species or reduced species to genus ratios may, therefore, be explained equally well by either predation or competition.

One community-wide pattern seems to incorporate both the effects of competition and predation: the ratio of the number of species of predators to the number of species of prey. This seems to be tightly limited in many communities (Cohen 1977; Briand and Cohen 1984). We have reservations about the observed excess of predators in these studies, which we argue is a reflection of the antipathy towards plant and invertebrate taxonomy on the part of many ecologists (Pimm 1982). Nonetheless, the constancy of ratios is impressive and is supported by the analysis of a better data base on freshwater invertebrates by Jeffries and Lawton (1984). (They, indeed, found many fewer predators than prey species.) Moreover, they argued that the constant ratios are most probably explained by "(a) the number of predator species being a function of the number of ... kinds of prey; and (b) the number of predators being constrained by competition between prey for 'enemy free space'."

Simply, these results suggest that predator to prey ratios might provide a simple, yet ecologically meaningful variable against which to relate the success or failure of introduced species. We may find that areas with deviant ratios are relatively easily invaded.

A caveat in applying this concept to fish communities is that most species pass through several trophic roles as they grow from larvae to adults. So one species can be both prey and predator to another species, depending on the life stage. In the extreme case, the predator to prey ratio would be unity. One alternative is to consider only adult trophic roles. In the context of species invasions, however, this may entail a sacrifice of important information, given the potential importance of predation on the juvenile stages of fishes for determining year-class strength (Sissenwine 1984). Another alternative is to limit the number of species considered; we can theoretically identify all of the potential predators of the invader (at all life stages), as well as all the potential prey of those predators, and it is the ratio of these variables that may be most meaningful.

Harvesting

Progressively removing a species through harvesting has an immediate effect: it creates a gap in the community structure. But it has some subsequent effects that may be less obvious. The total or partial removal of a species may cause other species losses, and such losses may cascade throughout the community. When these species losses cease, the community itself may not only just have fewer species, but have a structure that is no longer the result of a long process of community assembly. To fully appreciate the effects of harvesting, we must consider how communities respond to species removals and what this implies about their persistence, as well as the immediate effects of the gaps in composition created by harvesting.

Small gaps

The partial removal of a species obviously hurts those species that were predators on that species and benefits those species that were its prey. These effects favor invasions by species that are *similar* to the species being harvested, for such a species will be most likely to benefit from the reduction of the particular set of predators and the increase in the particular set of prey species. Of course, such an invader may still be in competition with our harvested species. But harvesting has an effect which is diametrically opposite those effects discussed so far, where

competition and predation from species present within a community tend to select for invaders that are *different from* existing community members. Now, if the invader is so similar to the harvested species that it, too, can be harvested in the same way, then the invading species gains no advantage from its similarity. So we conclude that the the most likely species to invade are those similar to the harvested species in all respects, except their propensity to be exploited.

This is a rather obvious conclusion, and the data for the Great Lakes seem to bear it out. From the original communities, native planktivorous fishes (coregonids) have collapsed under intense harvesting and have been replaced in the new communities by ecologically similar species (alewife, rainbow smelt) which are harvested less intensely because they are not as economically valuable.

How do the original and new community types differ in their persistence in the face of continued species invasions? Is it possible that these new communities might be essentially as persistent as the original ones because there have been one-to-one replacements of species? Indeed, might the new communities be even better because we have introduced salmonid species even more valuable than the lake trout? And, as the momentum for genetically engineered species increases, can we create even more valuable communities, through introductions following extensive harvests of less valuable species? We think it is more likely that these practices will lead to communities which are particularly vulnerable to species invasions.

Effects of removing a species

If there is not a one-to-one replacement of native with invader, we should ask what happens when we remove a species from a community? Can we neatly excise just one species or are there other effects? If there are other effects, what do these do to the communities' ability to resist invaders?

If we remove a species and the remaining $n - 1$ species persist, we call the community "species deletion stable" (Pimm 1979, 1980). There is a class of models where predators act in a compensatory fashion taking prey that are likely to die for other reasons (starvation, for example). Predator removals thus have no effect on the remaining species. But such models do not agree with nature, where the vast majority of predator removals cause changes — sometimes considerable ones — in the remaining species composition. Most multispecies models are not species deletion stable and neither are most natural aquatic ecosystems (Pimm 1979, 1980).

So what affects species deletion stability? Averaged over all the species in a model community, species-rich communities and communities with many interactions per species are less likely to be species deletion stable than model communities with few species and interactions. But species deletion stability depends critically on which species are removed from any web. While some species can be removed with few effects, the reverse is often true. For example, removing a specific top predator which preys on a generalized predator is likely to wreak havoc because, once released, the generalized predator can eliminate all but one of its prey species. Similarly, removing a top predator which feeds on several species which actively compete can also easily upset a coexistence that requires the predator to keep the superior competitor in check (Pimm 1980; Paine 1980). Such differential sensitivities to removal are embodied in the "keystone predator" concept, an idea that recognizes the critical role that some species play in maintaining community organization.

These theoretical studies look at whether species are lost or not, and not at *how many* species may be lost. For the models, we usually find that when we remove a species, another will be lost and its removal will cause other losses. How far will the effects cascade? The extent to which they do is an inverse measure of the community's resistance. The modelling results do not tell us directly, but they give a suggestion. If we remove top predators, communities that are species deletion stable have few species and few interactions between species; these are likely to be the end points of the cascade. Thus, when we remove top predators, species-poor, simple communities are probably not going to change as much as species-rich, highly connected communities.

In sum, species removals usually have a dramatic effect on the composition of the species at lower trophic levels. Very few natural communities appear to be unchanged when we remove top predators. Thus we can reject the idea that we can simply excise a single species from a system. Removing a species, especially a top predator, is going to seriously modify community composition.

Effect of serious disruptions on invasions

Given that removing a top predator will seriously disrupt community composition, we should now ask what are the consequences of these serious deletions to invasion. The answers may come from some studies of how communities assemble. A number of studies have recently "grown" food webs by starting from a simple community and then successively introducing species. Species that cannot increase when rare cannot invade the community. Keeping track of the proportion of such failures gives a measure of persistence: persistent communities will be hard to invade. Those species that can invade may displace one or more of the species in the community or simply add to the existing structure.

Post and Pimm (1983) assembled communities using an infinite species pool, while Drake (1985) used a finite pool of 125 species. Whether an infinite or finite species pool is more realistic depends on the relative time scales of invasion and evolution for a particular system. A finite species pool assumes that the assembly of the community is invasion dominated, a reasonable assumption for highly mobile species such as birds and fish. Both studies, however, found that invasion difficulty increased continually as species entered the community, even after the number of species remained constant. With the assumption of a finite species pool, Drake found that his communities became totally persistent: the community with a total of m species could not be invaded by any of the other $125 - m$ species (m was typically about 10). Of particular interest is that the m species were a different subset of the 125 species in different replicate runs. About 50% of the species were shared between pairs of these alternative communities. Drake found it impossible to reassemble any set of m invasion-resistant species without the help of other species. Apparently, some intermediate species, which later become extinct, are necessary for the assembly process.

The implications of these results seem clear. The number of species that coexist in a particular community must be a small proportion of the total number of species that can disperse there over the community's history. Yet most natural communities are highly persistent: their species composition is not changing dramatically. (We do not consider man-modified communities as "natural" communities in this context.) This suggests that natural communities are invasion resistant: what we see must be

the end points of a long process of species assembly. The historic communities of the Great Lakes may have been invasion resistant, although it is equally likely that they were still in a state of assembly and at least some invaders (e.g. the lamprey) could be integrated into the communities without the loss of native species (Christie 1974).

When we disrupt community composition, the resulting communities are no longer the end points of a long process of assembly. We have weakened the forces that prevent invasions, and we cannot expect the communities to be persistent. Moyle's (1986) analysis of California fishes confirms this expectation. Of 48 exotic species, 21 occur in highly modified habitats such as reservoirs and farm ponds, and another 21 occur in habitats such as streams with altered temperature and flow regimes. Of the remaining six species, four are salmonids introduced into fishless mountain lakes.

Given the disruptions to the historic communities of the Great Lakes, the new questions are (1) how invasion resistant are the present, transformed communities and (2) can we reassemble the original species into invasion resistant communities? If the new communities are invasion resistant, this can be good (they will persist) or bad (reintroductions of individual species will be difficult), depending on the long-term goals for the Great Lakes. It is likely, however, that the new communities will be less persistent than the original communities. Drake's results also suggest that reassembly of the original communities will be difficult, and will become more difficult with time. Moyle (1986) described the inability of native fishes to recolonize western lakes and reservoirs after these had been invaded by introduced species, even though a continuous supply of native recruits persisted in the feeder streams.

We note, in passing, that the results on community assembly come from some of the simplest multispecies models. The patterns of alternative communities arise from the interactions among a number of species. They do not come from the complexities of the population equations for any single species (such as those discussed by Peterman et al. 1979) that involve breakpoints and multiple domains of attraction.

Summary

Competition and predation have the potential for strongly modifying a species' chance of invading a community, so both can structure a community. There is an enormous literature on the patterns in community structure and the persistence it implies. But not only is this information very hard to interpret, it is *at best* indirect. Yet there are large data bases on species introductions which often document both success and failure. There are sufficient differences between taxa in the analyses performed so far that it would be rash to extrapolate their results to the Great Lakes. But there are many recorded fish introductions, and they open up the possibilities for many studies on community persistence.

Harvesting, in removing species, tends to cause gaps in the community that are most likely to be filled by species similar to those being removed. Of possible greater significance than the creation of these small gaps is the serious disruption of community composition we should expect when (especially) top predators are removed. Such removals typically lead to species losses that cascade through the community. The resultant community is no longer the end point of a long successional process. Both theory and observations lead us to believe that these seriously disrupted communities may be particularly vulnerable to species invasions.

Resilience, Variability, and Stress

From the long-term problems of community persistence, we now turn our attention to the short-term problems of population variability and how stress affects it. We define stress as any anthropogenic factor that has the effect of increasing the death rate of one or more age-classes in the population, or decreasing the birth rate. Harvesting, as well as pollution, falls within this definition.

As pointed out by Rapport et al. (1985), many symptoms, or effects, of stress are retrospective. Because fisheries are most often interested in maintaining a particular species mix, it is important to be able to detect and understand effects that are manifest at the relatively benign stages of stress if we are to consistently predict, rather than lament, disaster. A change in the year-to-year variability of a population is one potential early-warning mechanism and can signal subsequent, more permanent shifts in abundance. An understanding of this change in variability is also important because variability may contribute directly to the collapse of a population. An increasing amplitude of fluctuation can bring about a collapse in two ways: (1) densities may reach such low levels that recovery is impossible (Leigh 1979) and (2) fluctuations may bump a population out of a region of abundances where it is able to coexist with interacting species (the idea of domain stability) (Brauer and Soudack 1979).

The natural variability of fish populations can be considerable (Sissenwine 1984). The question is, how is this natural variability influenced by stress? The functional form of this relationship is not yet clear for any scale, although there have been speculations on its direction. The theoretical and empirical analyses on population variability that are useful in the context of this paper have followed three related tracks of inquiry:

(1) Examination of the relation between stress and population resilience or return time. Both resilience and return time are measures of how quickly a community returns to a previous state after a perturbation. The faster the community returns, the higher the resilience; mathematically, resilience and return time are inversely proportional.

(2) Examination of the relation between resilience and the variability of a population. Two hypotheses may agree on (1) yet disagree about (2).

(3) Direct examination of how stress affects population variability. This is the prevalent type of analysis in the fishery literature, since fishing effort is a relatively unambiguous measure of stress.

Stress and Resilience

The effect of harvesting on resilience has been studied by a number of fisheries ecologists (Beddington 1979; Beddington and May 1980; Doubleday 1976; Sissenwine 1977). A representative analysis was provided by May et al. (1978) who explored the relationship between increasing harvesting effort, return time, and population variability in single-species models. (Return time, the speed with which a population recovers from a disturbance to its density, is inversely related to resilience.) They considered a catalogue of eight recruitment functions widely used in fisheries modelling (Beverton-Holt, Fox, Chapman, Doi, Ricker, Logistic, and Pella–Tomlinson) and presented analyses of both the return time and the probability distribution of the catch as functions of effort.

The population models exhibited a monotonic increase in return time as effort was increased for six of the eight

recruitment functions. The return time of the model with a Beverton-Holt recruitment function could decease as effort increased towards the maximum sustained yield (MSY) value, but increased for effort greater than the MSY value; with a Fox recruitment function it remained constant for all values of effort.

This analysis considers only an increase in fishing mortality, and ignores the fact that harvesting can trigger compensatory mechanisms which may affect population resilience. Within an exploited population, the mortality rate increases with fishing intensity by definition. Specifically, this additional mortality is directed toward the larger individuals. In many cases, however, there are mechanisms which compensate for this increased mortality; these include increased prerecruit survival, a decrease in the age of sexual maturity, and an increase in the number of eggs produced per unit weight of female (or an increase in the pregnancy rate of marine mammals of given length) (SPOF 1983; Regier and Loftus 1972; Gulland 1971). These effects suggest that the resilience of a harvested population could increase, at least for the range of efforts over which the population is able to compensate for an increase in mortality.

Resilience and Variability

How do these proposed changes in resilience with increasing stress translate into variability in a population subject to random disturbances? Two seemingly reasonable approaches give diametrically opposite results (Pimm 1984b).

Alternative 1

In the analysis by May et al. (1978), random disturbances were incorporated into the model by making the intrinsic growth rate stochastic. They found that with all eight recruitment functions the standard deviation of catch (as associated with fluctuations in the population) increases as effort (E) pushes the catch towards MSY. This by itself is not surprising; the standard deviation of catch must increase from zero at zero effort. The coefficient of variation (CV, or standard deviation divided by the mean) of the catch or population size may increase or decrease, depending on the recruitment function. What *is* interesting is that as effort pushes the catch beyond the MSY (with resilience decreasing), the CV of catch always increases, the slope of this increase determined by the specific recruitment function.

A likely mechanism for these changes is that when the effect of environmental perturbations is density independent, resilient populations (i.e those that return quickly to equilibrium following a perturbation) are able to maintain more steady trajectories than populations with long return times. A population with a long return time will tend to be further from some average value (e.g. equilibrium) at the time of the next perturbation, and will thus reach more extreme abundances than a resilient population. This implies that if harvesting stress erodes the resilience of a population, which is what May et al. (1978) found, then its variability should increase with increasing stress.

This basic result has been found by several other modelling studies (e.g. Doubleday 1976; Sissenwine 1977) where noise was entered via density-independent terms.

Alternative 2

The relationship between return time and variability of the population and catch is reversed, however, if the effect of environmental noise is density dependent (e.g. a variable carrying capacity) (Shepherd 1977). In this case, a long return time renders the population less responsive to changes in environmental quality (it "sits it out" until more favorable conditions prevail), and so population variability is relatively low. A population with a short return time tends to track the variations in the carrying capacity, and is thus relatively variable.

There is another possible explanation for an inverse relationship between return time and variability. It is based on the assumption that the mortality rates (M) during the early stages of highly fecund (resilient) species are relatively high, so that only a relatively small change between years in these M values can produce a relatively large variation in recruitment. Presumably, the lower the fecundity, the lower the M, and the larger the variation in M necessary to produce a given variation in recruitment (as measured by CV).

A positive correlation between the degree of population fluctuations and fecundity has often been assumed, but satisfactory empirical evidence seems to be lacking (Spitzer et al. 1984). If the evidence can demonstrate that for fish populations, high resilience (as measured by fecundity and life span) indicates high variability, then we must still decide between the hypotheses which potentially explain this relationship.

Multispecies Models

The single-species results on the relationships between stress and resilience, and between resilience and variability, neglect the possibility that interactions between species have an important effect on these relationships. We therefore need to ask how species interactions modify the single-species results. To do this, we considered a two-species, predator-prey, Lotka-Volterra model with proportional harvesting, as part of a study to be published separately.

Given a perturbation to the species densities, an oscillatory return to equilibrium is likely for this model. The existence of these oscillations are especially interesting, since they can interact with stochastic fluctuations in the environment to produce population cycles (Nisbet and Gurney 1982). If the model oscillates, then as effort increases, the period of these oscillations tends to increase until some value of effort before the predator is driven to extinction.

As long as the model exhibits oscillatory behavior, then the return time is a nonincreasing function of effort: it decreases for predator harvesting and remains constant for prey harvesting. To examine the relationship between harvesting and population fluctuations, we introduced random fluctuations (henceforth called noise) into a discrete time version of the oscillatory model. Noise was modelled by perturbing predator or prey densities by a random fraction of their previous values, the time intervals between perturbations being exponentially distributed. The results of the behavior of the populations' CVs with increasing effort were as follows:

(1) Predator harvested, noise on the predator: the predator population's CV decreased before finally increasing.

(2) Predator harvested, noise on the prey: the predator population's CV increased monotonically.

(3) Prey harvested, noise on the prey: the prey population's CV decreased slightly before finally increasing.

(4) Prey harvested, noise on the predator: the prey population's CV decreased monotonically.

The multispecies view cannot at this stage predict the relationship between population variability and stress. One problem is whether environmental noise acts on a population, through its prey, its predators, or directly. Noise acting through predators seems quite important (Sissenwine 1984). Our model

does suggest, however, that the stress/variability relationship will not be the same for different species in the community.

Stress and Population Variability: Empirical Results

Simply, there are so many factors that theoretically can affect the relationship between stress, resilience, and variability that we are unable to draw any definite conclusions about the form that this relationship takes. Although continued theoretical work is certainly needed, resolution of the hypotheses presented above ultimately depends on the analysis of empirical data. We will limit our discussion to some representative data analyses of the stress/variability relationship in fishery systems, and argue that these analyses are oversimplified and probably misleading.

A type of analysis suggested by Regier and Loftus (1972) and used by May et al. (1978) to support their argument that variability increases with stress is to simply plot catch (C) against effort (E). A good example can be constructed from the data on redfish (*Sebastes marinus*) from Mayo and Miller (1976); these data were plotted by May et al. (1978). This plot appears to show increasing variability of catch about the fitted curve as effort increases. These graphical arguments must be viewed with caution, however, for three reasons. First, the standard deviation of catch *must* increase from a value of zero at zero effort, irrespective of any model. So the increasing scatter in the figures supports no particular relationship between stress and variability.

Second, the theoretical arguments discussed above consider that catch variability mirrors population variability, which is changing as the community is stressed. So, it would be more appropriate to consider directly the relationship of population abundance to effort. In most cases, however, an index of abundance such as catch-per-unit-effort (CPUE) must suffice. Using the redfish data, we grouped efforts into "low" and "high" categories about the median effort. When we compared coefficients of variation in CPUE in the two groups, we found them to be almost identical.

Third, although the variability of the two groups is nearly identical, the groups differ in an important way. When we examined in what years low and high efforts occurred, we found that the high efforts tended to be associated with three major downward trends in CPUE. In contrast, the variation at low efforts had a relatively small trend component. If it is characteristic of a fishery that periods of high effort produce distinct downward trends in population abundance, then this may result in high efforts being associated with high variability. Trends can inflate any measure of variability because often, a given number of data points span a wider range of values when part of a trend than if there were no trend present. In general, data analysis pertaining to the relationship of population or catch variability with harvesting stress that does not include a time component is potentially misleading.

The failure to separate different time scales of variation is an important source of error also in across-population comparisons. The Strategic Planning for Ontario Fisheries (SPOF 1983) working group has attempted to identify an index of stress based on the CVs of population abundance indices over time for various combinations of species and lakes. One of the largest differences between populations comes in comparing the CVs for walleye (*Stizostedion vitreum vitreum*) in Lake Erie and Escanaba Lake; it would appear that the more heavily stressed population in Erie (1948–61: CV = 0.63) is more variable than the one in Escanaba (1955–72: CV = 0.36). But this analysis is misleading; although the high coefficient of variation for CPUE of walleye in Lake Erie is associated with a high level of stress, 69% of the total variation about the mean is explained by a crude long-term trend. The downward part of the trend is the collapse of the walleye fishery; this leads us to the trivial observation that collapsing populations are highly variable, and the index of variation thus has no additional predictive power.

In contrast, in Escanaba Lake the relatively low CV for walleye numbers is associated with a relatively low-stress community. There is no significant trend in the data, however, and essentially all of the variation is due to short-term fluctuation.

It is clear that an uncorrected CV for a given time period is too crude to provide a comparative index of population stress, since it includes the variation due to both trend and short-term components. Distinguishing the trend component from the short-term component of variability is important because the variation at these different scales may be the result of different causative factors, or one factor may affect the variation at each scale differently. If populations are to be compared with respect to their variability, the variation due to each component should be calculated separately, as we have done in Fig. 1. What happens to the variance *about* the trends is clearly not resolved by the analyses we have discussed.

Summary

Single-species models with stochastic environmental variation usually predict that population variability increases with increasing fishing intensity, if the noise enters the model via density-independent parameters. If the noise enters via density-dependent parameters, then the opposite result is obtained. Both alternatives can be associated with either (1) a monotonic increase or (2) a decrease and then an increase in return time with increasing effort, depending on the model used. A similar analysis using a predator-prey model suggests not only that return time may be likely to decrease with increasing effort, but more importantly that the direction of the change in population variability depends on the relation of that population to other species within the community. Moreover, with multispecies models, the populations may oscillate and the periods and amplitudes of those oscillations may change with harvesting.

The analyses of fisheries data that attempt to adjudicate the various theoretical predictions are often inadequate because they fail to account for the behavior of the fishery over time and to distinguish between different temporal scales of variation. Variation due to trend components of a time series may be more often associated with high-stress than with low-stress fisheries (because of both direct and community effects), causing apparently higher variation with increasing stress.

Resistance

Given that harvesting and pollution cause species losses, how radically will the communities' species composition be changed by these losses? And what will happen following species invasions? Rather than species composition, it may be the ratio of the biomasses of a set of species before and after species removal or introduction that should be of interest. Whether total biomass or species composition is more interesting will depend on the relative commercial values of the species. If these values are broadly similar, then it will be their total biomass that matters; if some species are much more valuable than others, then it is the resistance of species composition that may be

crucial. Now, while species composition may change dramatically following species removals, total biomass may not. And, indeed, there appears to be a negative correlation between these two measures of resistance to species removals.

Species Composition

We have already discussed resistance to species removals when we considered invasions. We noted that communities are not resistant to removals of top predators: they tend to change a great deal. What happens when we consider the effects of species additions on the species composition of the former community?

Given a successful introduction, there could be no, few, or many species losses, at the same trophic level as the introduction or the levels above or below it. What do models say about how community properties affect these losses? And how do the data relate to these models? To our knowledge, there are very few attempts to answer these questions. One synthesis of empirical results is that of Simberloff (1981) who reviewed 10 papers covering over 850 plant and animal introductions. Although the data differ widely in quality, there are two patterns which apply to all the studies:

(1) Less than 10% of the introductions caused species extinctions (there were only 71 extinctions). Greenway (1967) reported the highest percentage (30%: this involved 55 of the 71 extinctions) and he was principally concerned with avian extinction. Introductions tend to add species to a community rather than to cause losses.

(2) Both overall and within Greenway's study, predation was the principal cause of extinction (50 of 71 and 42 of 55, respectively). Habitat change accounted for 11 of the 71 extinctions; competition from the introduced species was a distant third, with 3 extinctions.

Simberloff argued that on average, "natural" communities appear highly resistant to successful species introductions: most introductions add species to a community, rather than cause extensive extinctions. This conclusion, however, has been sharply criticized (Herbold and Moyle 1986; Moyle et al. 1986), especially with regard to invasions of fishes.

Some introductions, *Cichla* into Lake Gatun, Panama (Zaret and Paine 1973), for example, clearly have a devastating impact on the community. In fact, extinctions and severe declines of native species are a fairly common occurrence following the establishment of introduced fishes (Moyle 1986). What then explains this discrepancy with the results of Simberloff (1981)? Herbold and Moyle (1986) cited four key criticisms of Simberloff's analysis: (1) in most cases, the authors of the review papers used did not address the issue of competition, although criteria for interspecific competition are used by Simberloff to define an "effect" of introduced species; (2) Simberloff's determinations of no effect are generally in conflict with the conclusions of the reviewed authors; (3) many of his examples of no effect were derived from references in which the impacts of introduced species on natural communities were not mentioned, thus equating "no mention" with "no effect"; and (4) much of the perceived lack of evidence of the negative impact of introductions may be due to a lack of knowledge about the time scales of species displacement and a lack of follow-up studies.

Some communities may be resistant, but others are spectacularly vulnerable. We clearly do not understand what community-level properties determine the degree of further species changes once a species successfully invades a community. A synthesis of the effects of species introductions, like Simberloff's, but paying attention to the criticisms of Herbold and Moyle, is needed urgently.

Biomass

We know of no studies that review the changes in the total biomass of a set of species following species introductions. The problem of species removals, however, has been investigated. Theoretical studies show that increased competitive interactions, a relatively small number of species, and evenness of species densities all decrease the change in total biomass following a predator's removal (King and Pimm 1983). Roughly speaking, the greater the proportion of species competing, the more likely changes caused by the predator's removal will be compensated by changes in competition. Competition can be proportionately greater among small numbers of species and tends to result in more evenly distributed densities. In general, these results are in contrast with those involving the effects of removals on species composition. Indeed, for some model systems, large changes in biomass are associated with small changes in composition and vice versa (Pimm 1984a).

These effects have been demonstrated experimentally for terrestrial grazing systems (McNaughton 1977). Data we are currently assembling show they are also features of a wide variety of marine and aquatic systems. The results also seem reasonable in the Great Lakes context where species composition has changed dramatically, but total yields have remained relatively constant.

Summary

Our assessment of the resistance of a community to further change, given species removal or introduction, will depend on our measure of resistance. Species removals, especially of top predators, tend to drastically alter the composition of the remaining community. Community properties that create these cascading losses may, however, insure relatively minor changes in total biomass. Species introductions, in contrast, do not seem to bring about extensive extinctions in many communities, although introductions can, on occasions, be devastating. It seems clear, however, that the resistance of a community can be drastically eroded by stresses such as harvesting and pollution; this may involve no more than allowing a top predator to be removed as a consequence of invasion. The subsequent losses of species lower in the food web allow further invasions to occur.

Conclusion

The central theme of this paper is that we can characterize population and community dynamics in general ways and so seek an understanding of those characteristics. The population and community are simply different levels at which we observe the effects of species interactions. For example, the successful introduction of an exotic species to a community may be characterized both by the change in community composition and by changes in long-term trends in population abundances. Clearly, humans also must be considered as an interacting species; we compete with and prey upon a variety of species.

We have attempted to characterize the principal dynamics of interest using four facets of stability: persistence, resistance, resilience, and variability. We have asked how persistent are communities to species invasions, and how resistant are they to further changes, given invasions or losses. We have also

considered the resilience and variability of individual populations. We can inquire what are the properties of one system that make it less persistent, resistant, resilient, or variable than another. These questions are at once both interesting and realistic; we can proceed with reasonable confidence that the appropriate data can be gathered and tests be made. In this paper, we have begun to answer these questions using current ecological theory.

One generalization has become exceedingly clear; these four aspects of stability can be strongly influenced by stresses such as harvesting and pollution. Stress can lower community persistence; the probability of an invasion seems to increase as the community is disrupted (e.g. when small gaps are formed). Stress can also lower community resistance. Once an extinction does occur, the cascade of effects will be magnified if many species are already at low abundances. Moreover, the resulting transformed community may have low persistence relative to the original set of species which was the result of an assembly process. We have also seen that harvesting is predicted to influence both population resilience and variability.

What all these considerations suggest is that there can be no simple answer to the question of what determines ecological "stability." There are many things meant by stability and many factors affect those things. But, broken into its component parts, ecological stability becomes a set of questions that we may attempt to answer. We think that this "divide and conquer" approach is a promising one, if only because the many unanswered questions in this paper do have the potential to be answered by syntheses of existing knowledge.

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Ecosystem Science for the Great Lakes: Perspectives on Degradative and Rehabilitative Transformations

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Conventional approaches to ecological management presuppose the preeminence of normal natural processes in quasi-equilibrium state, in the presence of one or a few cultural stresses of light to moderate intensities. They also presuppose that the abiotic and biotic structural form of the ecosystem is relatively unaffected. In some parts of the Great Lakes, normal natural ecosystem processes have been overwhelmed by numerous intense cultural factors. Rehabilitation of such areas requires information and understanding of a type that is not central to conventional fisheries biology. We review and extend existing scientific approaches that contribute to an effective and relevant "ecosystem science," according to the criteria that they (1) incorporate spatial and structural models appropriate to an ecosystem perspective of the Great lakes basin, (2) incorporate functional attributes actually observed in stressed and culturally degraded aquatic ecosystems, and (3) provide information directly relevant to effective, informal, broadly based mechanisms of ecosystem rehabilitation and husbandry.

Les approches classiques à la gestion écologique supposent la prépondérance de processus naturels normaux presque à l'état d'équilibre en présence d'une ou de quelques contraintes d'origine humaine d'intensité légère ou modérée. Elles supposent aussi que la structure abiotique et biotique de l'écosystème soit relativement peu modifiée. Dans certaines parties des Grands Lacs, les processus naturels normaux de l'écosystème n'ont pu résister à divers facteurs intenses découlant de l'action de l'homme. La restauration de telles régions suppose de disposer d'un type de renseignements et de connaissances ne présentant pas d'intérêt particulier en biologie classique des pêches. Les auteurs analysent et développent les approches scientifiques actuelles qui contribuent de façon efficace et pertinente à la «science des écosystèmes» dans la mesure où elles 1) font appel à des modèles spatiaux et structuraux appropriés à l'écosystème du bassin des Grands Lacs, 2) tiennent compte de caractéristiques fonctionnelles notées dans des écosystèmes stressés et dégradés par l'action humaine, et 3) fournissent de l'information directement axée sur des mécanismes de restauration et des gestion de écosystèmes qui soient efficaces, souples et généraux.

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Nowadays perhaps a dozen approximations to an "ecosystem approach" are under development for management of the Great Lakes (Lee et al. 1982) and for marine systems (Squires 1983; Kerr et al. 1985; Ulanowicz and Platt 1985; Ray 1985). These derive from different traditions of engineering, geography, hydrology, toxicology, fisheries, limnology, climatology, etc. (NRC/RSC 1985). Other approaches relating to both terrestrial and aquatic systems have recently been described (Odum 1983; Likens 1984; Risser 1985; Barrett 1985; Loucks 1985; Margalef 1985). These approaches share a loosely analogous set of concepts and presuppositions that differ somewhat from much of conventional applied ecology.

As they are conventionally practised, applied ecological approaches focussing on trophic dynamics, population dynamics, or ecotoxicology are insufficient to comprehend the degradation or rehabilitation of the Great Lakes. These approaches implicitly presuppose the preeminence of normal natural ecological processes in the presence of one or a few cultural stresses of light to moderate intensity, and that the biotic and abiotic structure of the ecosystem is relatively unaffected. Management efforts based on these "subdisciplines" of ecology have been applied with partial and varying success to problems of ecosystem degradation in the Great Lakes basin: trophic dynamics to manage eutrophication, population dynamics to manage exotic fish species such as Pacific salmon, and ecotoxicology to manage and control toxic contaminants. But alone or together they lack the diversity of concepts and methods that an effective science for Great Lakes ecosystem rehabilitation requires.

In some parts of the Great Lakes, normal natural ecologic and geomorphic processes have been overwhelmed by numerous intense factors of human origin. Locations such as Hamilton Harbour, Toronto Harbour, Green Bay, and others have been identified as "areas of concern" (IJC/WQB 1985) and have been slated for remediation, or partial abatement of ongoing abuses. The purpose of this paper is to review and extend the science available for the scientifically and socially more comprehensive processes of ecosystem rehabilitation and husbandry of such areas and of the Great Lakes basin as a whole.

Kerr (1982), Rigler (1982) and others have clarified the role of external study of integrated systems, and the usefulness of attempts to understand the integrated properties of systems before undertaking explicative internal analyses. Research

programs that neglect comparative and historical study of ecosystems are not likely to provide insights that are directly useful to ecosystem science, although they can provide information on population dynamics, organismal physiology, or other subecosystem phenomena.

The development of ecosystem science that combines both internal and external perspectives, or what Rapoport (1986) called analytic and holistic approaches, requires information and understanding of a type that is not central to conventional ecology. Ecosystem science should (1) undertake comparative and historical study (see Gould 1986) of healthy and degraded ecosystems, (2) seek an understanding of the effects on ecosystems of human culture at local and regional scales, and (3) address the implementation of scientific knowledge relevant to ecosystem degradation and rehabilitation. It should do these things within a coherent and rational body of concepts and practice.

Here, we sketch such a perspective. It shares some general analytic and holistic features of "stress ecology" (Odum 1985; Rapport et al. 1985) and design features of landscape ecology (Dorney and Hoffman 1979; Forman and Godron 1981; Dorney and McLennan 1984). We begin by reviewing some scientific approaches that we feel to be particularly relevant to recognizing and understanding key structural and functional aspects of aquatic ecosystems under intense human influence. Next we discuss the nature of ecosystem rehabilitation, the options associated with it, and the relative roles of analytic, holistic, and design aspects in scientific study and management of degraded aquatic ecosystems. We conclude by considering the role of cooperative, noncentralized, nonhierarchical mechanisms of aquatic resource allocation in the implementation of ecosystem science.

Approaches to the Study of Structure in Aquatic Ecosystems

We use the word "structure" in the sense of Bertalanffy's "dynamic morphology," recognizing that structure and function are related concepts; structures represent slow processes, and functions represent faster processes (Bertalanffy 1950; Davidson 1983). Ecological structure encompasses all "slow" ecosystem processes, especially those which contribute to three-dimensional spatial complexity, although it is also recognized in long-term consistency of species representation in coevolved or "harmonic" communities in relatively unstressed ecosystems (Ryder et al. 1981; Hecky 1985).

The following concepts and empirical generalizations seem particularly relevant to an ecosystem approach to Great Lakes ecosystem rehabilitation. They have a common feature in that they all seek an understanding of external (energetic, geologic, geomorphic, meteorologic, geomorphic, hydrologic) control of ecological phenomena — the "templet" of Southwood (1977). We would add consideration of human effects in these models, emphasizing the broad and pervasive linkages between the human-terrestrial and aquatic ecosystems (Christie et al. 1986).

Self-Organizing Systems in Ecology

Modern systems approaches to ecology share some of the organismic ideas that interested the late Ludwig von Bertalanffy, not an ecologist himself, but one of the "fathers" of general systems theory (Davidson 1983). Foremost among these ideas are open systems, which continuously exchange matter and/or energy with their environment; equifinality, in that open systems may reach the same end point from different starting points and in different ways; and anamorphosis or self-organization, the tendency for an open system to evolve towards increasing complexity and functional capability, at least in a benign environment (Bertalanffy 1950; Davidson 1983).

As proposed by Bertalanffy, self-organization is a property exhibited by complex, energetically open systems. Through the theory of open-system thermodynamics (i.e. Prigogine 1978; Allen 1985), self-organization is being explored on a variety of scales. There is growing interest in the possibility that concepts of open-system thermodynamics may be analogous or homologous to some concepts of ecosystem development and biological evolution. Living organisms appear to possess some of the features of dissipative structures; they take in energy of low entropy, use it to do work such as the building of cells and tissues, and release energy of higher entropy. Johnson (1981) has suggested that only population-like groups of organisms within a species (ecodemes), which are continuous through time, and are able to undergo adaptive change, can function as dissipative structures. In this context, Johnson formulated a general theory of ecosystem development and evolution, in open-system thermodynamic terms. Johnson's schema and that of Wiley and Brooks (1982) represent important attempts to relate ecosystem structure and development to patterns of energy flow through systems at various levels of complexity.

The Rawson Perspective

Figure 1 is based on a schema developed by Rawson (1939) (see also Larkin 1974) to provide a conceptual framework for understanding the limnology of lakes as it relates to productivity of valued fish species. Nowadays, in parts of the Lower Great Lakes, virtually all of the elements of Fig. 1 have been strongly modified by humans. In recent decades, hundreds of papers have been published that relate to various of the limnological interrelationships indicated in Fig. 1 (e.g. see Oglesby 1982 for a review of fisheries production as affected by some of these interrelationships). Somewhat similar schemata have been developed for streams and rivers (Platts 1979; Vannote et al. 1980; Karr et al. 1985). General characteristics of this rather common perspective of natural systems were summarized by Russwurm (1974).

Land–Lake Continua

The River Continuum Concept (RCC) of Vannote et al. (1980) and subsequent correctives (Statzner and Higler 1985; Minshall et al. 1985; Frissell et al. 1986) provide a mapping of biological organization onto the geomorphic structure and hydrodynamic processes of relatively undisturbed river systems, emphasizing the interaction (via hydrologic patterns, light, organic material, and sediment inputs) of the stream system and the surrounding landscape. With its theoretical origins in the application of Bertalanffy's (1950) ideas to fluvial geomorphology (Chorley 1962; Leopold and Langbein 1962), the RCC interrelates open-system approaches in geomorphology and ecology. It may be expanded to relate the functional linkages of interest when describing the interactions of Great Lakes ecosystems and their human inhabitants, namely the linkages of structure and process that unite the land, streams and rivers, and nearshore lake waters as components of the same open system (a land–river–bay–lake continuum).

Legendre and Demers (1984) reviewed the emergence of

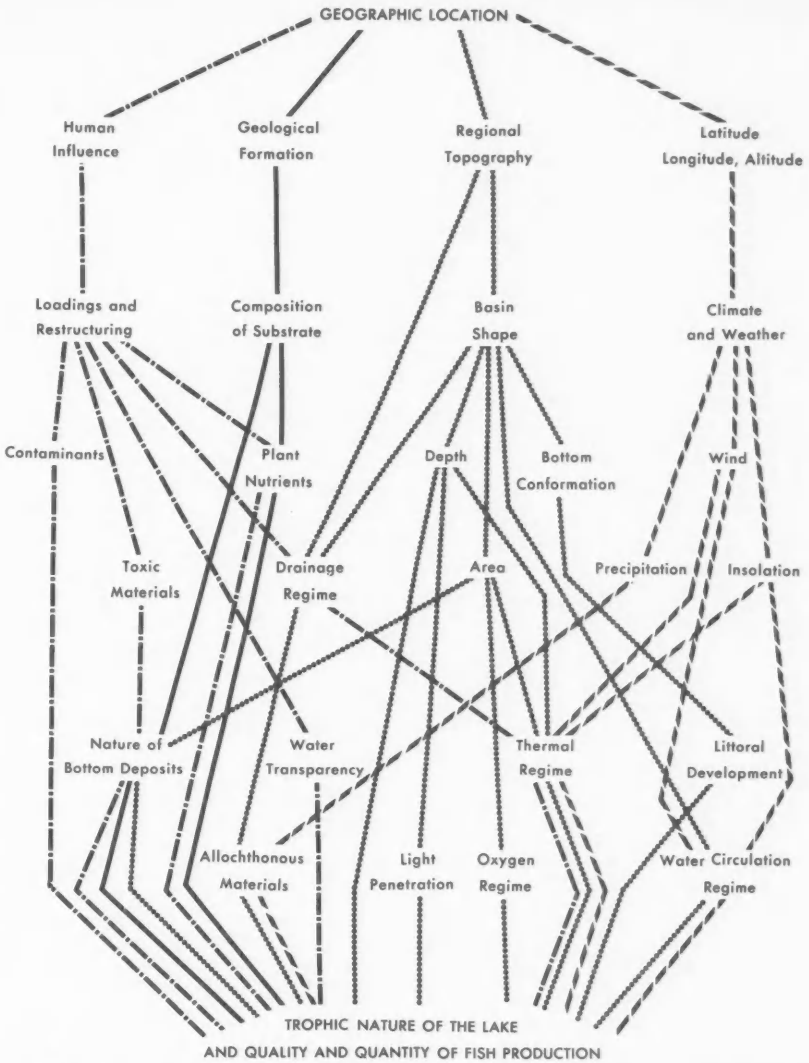

FIG. 1. Various human and abiotic factors that influence the biotic characteristics of lakes, especially with respect to the ecological production of fish of various species. This is a modified version of D. S. Rawson's diagram (Rawson 1939; see also Larkin 1974, p. 51); the modifications involve primarily a further elaboration of the "Human Influence" factor, which was sketched in a very simple form in the original diagram.

"dynamic biological limnology," or "dynamic biological oceanography," which is in many ways an open-water analogue to the coupling of abiotic and biotic structure envisioned for rivers by Vannote et al. (1980). The perspective of Legendre and Demers recognizes hydrodynamics as the driving force of open-water aquatic ecosystems, in that the physical, chemical, and biological factors of the open-water environment act as the factors through which hydrodynamic variability and pattern are expressed in living organisms. The couplings of the abiotic organization (i.e. horizontal and vertical mixing patterns) and biotic organization (i.e. life cycles, aggregation behaviour, and physiological responses) are closely dependent on the relative spatial and temporal scales of these processes.

Centres of Structure and Organization in Great Lakes Ecosystems

Certain features or subsystems may be more important than others to the health and survival of Great Lakes aquatic ecosystems. Such areas have been called "environmentally sensitive areas" but that concept, while often useful, is not sufficient to convey the message that we advocate here. Relatively small or localized areas that provide essential conditions for breeding, spawning, rearing, and feeding of fishes do not always appear to be "environmentally sensitive" and may have an ecological role far more important than would be suggested by their size alone. In temperate aquatic ecosys-

tems such as the Great Lakes, areas which we here designate as "centres of organization" tend to occur in the coastal or nearshore zone and exhibit distinctive combinations of abiotic and biotic characteristics.

The structural aspect of these centres results from the interaction of physical and biological processes involved in water movement, geomorphology, and development of vegetational strata. One of these factors may predominate locally: it may be primarily biotic form such as stratification in forest ecosystems, plants in wetlands and marshes, invertebrate colonies in coral reefs, or it may be primarily abiotic form such as river meanders, rocky shoals in glacial lakes, or open-water hydrodynamics.

In the Great Lakes, the structural and hydrologic features of diverse river channels, complex coastlines, rocky shoals, estuaries, and coastal wetlands are such that in a natural condition (1) substrate and sediment accumulations are of a size and arrangement that provide clean, well-oxygenated substrate surfaces and interstices and/or sediments suitable for the establishment of aquatic plants and (2) disruptions by currents, wave action, ice movement, seiches, or floods are of a frequency, intensity, and predictability that allow a variety of plants and animals to colonize the area, either for the entire life cycle or for certain vulnerable stages (embryonic, juvenile, etc.) of the life cycle. With respect to native, valued species of Great Lakes fishes, the most important requirements of the early life stages, provision of oxygenated water and protection from predation (Kryzhanovsky 1949; Balon 1975, 1985), are best met in these types of areas.

Wetlands, and to a lesser extent also the other areas that serve as centres of organization, act to modulate various forces and flows across the land–water interface. Modulation occurs with respect to physical or hydrodynamic forces (floods and seiches), chemical flows (nutrients and contaminants, usually from land to lake), and biological flows (movements, migrations, growth, and reproduction of fish, birds, mammals etc.).

In the long run the wetlands, side channels, estuaries, etc., may be neither sources nor sinks of chemical or other materials that are transported back and forth across the land–water interface (Sager et al. 1985). But they appear to export "information" or "negentropy" in the form of the young stages of large organisms reproduced there, that subsequently move within the ecosystem to exert regulation or control through "top-down" biological interactions (Shapiro 1980; Tarapchak and Nalewajko 1985) such as feeding, predation, or competition. Examples from Great Lakes wetlands may include the young of large benthic fish (esocids, centrarchids, some percids) that move about within and beyond the wetlands to forage on more pelagic species (cyprinids, clupeids, osmerids) that seem to be less tightly linked to centres of organization.

In the Great Lakes basin, as elsewhere, there has been widespread destruction of nearshore and tributary structural features through activities such as shoreworks, channelization, land clearing, landfilling, land drainage, rock removal, dredging, and siltation. The remaining locales that we consider to function as ecological "centres of organization" are indeed becoming identifiable as discrete and often isolated entities, probably much more so than would have been the case 200 yr ago when such features dominated much of the Great Lakes nearshore zone. In many areas, especially near older settlements, these features have been altered for so long that our best information about original conditions comes from historical maps and descriptions (i.e. Whillans 1979; Sedell et al. 1982). Local and stock-level effects of these activities have been inferred (Huntsman 1944; Schneider and Leach 1977; Whillans 1979; Holmes and Whillans 1984).

Ecosystem Response to Stress

Ecological Succession and "Stress-Response" Ecology

The concept of succession is used in several senses in ecology. Perhaps the oldest connotation refers to the sequence of species populations in an ecosystem, through time (Clements 1916; cf. McIntosh 1980). In subsequent use this basic idea has been associated with changes in diversity, structural and functional complexity, and self-regulation and has been applied to both primary succession of a new habitat as on a lava flow or following retreat of a glacier and secondary succession in an ecosystem following a period during which it had been subjected to some natural disruption that had altered the state of the ecosystem away from its initial state. Another, more recent use refers to secondary or recovery succession following relaxation of a harmful stress after a period during which the system had been subjected to unnatural or cultural disruption.

Ecosystem succession or development may be constrained or opposed by disruptive influences such as physical disturbance, excessive nutrient inputs, poisoning, harvest, etc. — or "stress" (Margalef 1968, 1975; Regier and Cowell 1972; Odum et al. 1979; Odum 1981, 1985; Cairns 1982). Stress is interpreted as a resetting influence; when applied intensely to a "natural" ecosystem that had developed in a benign environment, it forces the ecosystem to a different state. With most kinds of stresses the modified state has some of the features of an earlier successional state, but also exhibits some additional features or "diagnostic pathological symptoms." When intense, most kinds of cultural stresses cause the destruction or crippling of some ecosystem components and what may be termed "pathological rejuvenescence."

Stress may be beneficial or detrimental to long-term ecosystem health, depending on the nature, timing, frequency, duration, and intensity of the stress and depending on our value judgements of ecosystem attributes relating to "health." The changes that occur in stressed ecosystems do not necessarily represent compensatory adaptation in a physiological or evolutionary sense, but rather represent shifts in species representation and interaction as dictated by the scope and nature of the new environmental conditions. The biotic association that establishes itself may develop some self-regulatory processes that may resist processes of recovery to a more natural state, should the stresses be relaxed.

Natural regimes of stress or disruption are important in maintaining certain ecosystems or portions of ecosystems in states that exhibit some features of early stages of succession. Many examples of this have been documented with respect to marshes, the boreal forest, grasslands, etc. Some "natural" stresses have been called "subsidies" by Odum et al. (1979) and "eustresses" by Rapport et al. (1985).

A General Stress Syndrome

Various kinds of stress or ecological disruption tend to result in similar ecological symptoms within and among ecosystems, although each type of stress–system interaction will also have unique symptoms. With respect to the sorts of symptoms shared by different kinds of stressed ecosystems, a general stress syndrome may be recognized as a whole-system manifestation

of decreased ecological structure, complexity, or organization, brought about by external forces (Rapport et al. 1985). The generality of ecosystem response to stress was inferred from comparative whole-system or "external" studies of responses of somewhat similar ecosystems to a variety of degradative stresses of human origin.

A general stress syndrome, typical of "abused ecosystems," consists of such symptoms as reduced efficiency of nutrient cycling, changes in productivity, reduced species diversity, reversed successional sequences, changes in the size distribution of species (in stressed aquatic systems, large, long-lived benthic species are often replaced by small, short-lived pelagic species), increased incidence of disease, and increased amplitude of population fluctuations (Woodwell 1970; Paloheimo and Regier 1982; Odum 1985; Rapport et al. 1985). In general, these symptoms indicate the reverse of those trends that Bertalanffy described as occurring in complex self-organizing systems in a benign environment, i.e. progressive centralization, the tendency for certain subsystems to become dominant; progressive differentiation or mechanization, the tendency for certain subsystems to become more specialized or limited to single functions; and progressive integration, the tendency for subsystems to become more dependent on the whole system (Davidson 1983).

Severe degradation may destroy key ecosystem components and inactivate the normal processes that drive ecological recovery or succession, thus causing "pathological rejuvenescence," e.g. infilling of a wetland, species extinction, and desertification.

Discontinuities in Stress-Response Function

The following examples are indicative of some degradative transformations that have occurred in the Great Lakes. We will use the association of fish taxa – what is often termed the "fish community" – to show how the biotic parts of an aquatic ecosystem have responded to intensifying stresses that may be focussed initially on the fish themselves (as in fish harvesting or selective fish poisoning) or on other features of the ecosystem (as in the removal of gravel from bars used as spawning shoals, nutrient enrichment leading to eutrophication, stream damming, etc.). These examples indicate how the response of a fish community to intensifying stress may be gradual over some range of the stress, but may be quite dramatic, discontinuous, or "catastrophic" over some other range of the stress. The response function to a waning or remediation of stress may not coincide with that of a waxing stress, leading to hysteresis or catastrophe cusps (Zeeman 1976) of some kind, even under gradual regimes of stress imposition or relaxation. Researchers have only recently begun the study of the generalized responses of the Great Lakes fish community to regimes of waxing and waning cultural stresses. Here we sketch some tentative, approximate inferences.

Fishing

Some fishing practices effect discontinuous qualitative changes in the fish association. For example, a fishing weir may be placed so as to intercept virtually all spawners of a stock with a result that this stock is eliminated. If, as is often the case with salmonids, the stock acts in some respects as an ecologically unique taxon, then the diversity of the fish community is impoverished by such an effect. The number of such ecotaxa as a measure of community diversity would be reduced discontinuously. If the weir were then removed permanently, a similar or comparable new ecotaxon might eventually develop, but that event might require decades if not centuries of time according to present information. A realization of the problems involved in barring spawning runs led to regulations in some Great Lakes jurisdictions over a century ago against setting of fish gear near the mouths of streams or in some offshore fish sanctuaries which included important spawning reefs.

Consider a less simple, less graphic example that relates to the mesh size of fish nets used, whether of entangling gear such as gill nets or of entrapping gear such as trap nets. In the unstressed natural Great Lakes, perhaps over 50% of the biomass of the entire fish community was contributed by fish each over 5 kg in mass (see Regier 1979). The most efficient gillnet mesh for such larger fish was well over 12 cm stretched measure (or over 4.5 in. stretched measure). As the large fish, notably the most desirable lake trout, lake whitefish, and walleye were "fished up," the fishermen gradually shifted to smaller mesh sizes. Through trial and error it gradually came to be recognized that mesh of 12 cm was a kind of break point: where smaller mesh was used, some unpleasant consequences happened. Lake trout gradually diminished in abundance and whitefish and walleye populations became unstable with boom and bust year classes. Thus, mesh sizes could usually be reduced from 14 to 13 to 12 cm without marked response of the fish association, but when it was reduced to 10 cm, a kind of discontinuity of response became apparent with the loss of one taxon and a shift into a domain of marked instability of other taxa. (See Regier and Loftus (1972) for more details of this phenomenon.)

Eutrophication

As with the effects of fishing on the fish association, the effects of eutrophication due to loading of plant nutrients have been studied scientifically for about a century now. But eutrophication was not often distinguished from pollution that included organic material and other wastes, until about 1950. The role of oxygen concentration with respect to the well-being of the fish community is well known. In some stratified lakes, the catastrophic response regime of eutrophication as related, say, to the concentration levels of oxygen in the hypolimnion has been understood for about 50 yr, and the implications to cold stenothermic fish species of such lakes were then quickly understood (e.g. with respect to the salmonines and coregonines of the lakes of the European Alps).

Some direct evidence (as in the central basin of Lake Erie, see Barica 1982) and much indirect evidence indicates that year-to-year differences in meteorologic and hydrologic regimes affect the intensity of relative anoxia as eutrophication reaches intensities at which a shallow but stratified lake basin may shift from oligotrophy to eutrophy. Thus the discontinuity of response relates to shifts from a quasi-equilibrium character of community interactions to relatively highly turbulent instabilities. These instabilities tend to be damped when the aquatic ecosystem is driven fully into the domain of the eutrophic where even an unusual, favourable coincidence of meteorology and hydrology does not cause a return to levels of oxygen concentrations minimally sufficient for cold stenothermic fish.

With intensifying eutrophication the effect on salmonines apparently is one of withering away, while coregonines may go through a period of violent population fluctuations and perhaps some genetic introgression of closely related species before the final extinction of the entire coregonine taxocene.

Loading by putrescible organics

When nontoxic organics with high biological oxygen demand are loaded into streams or rivers, the effect is to foster a community of decomposer organisms that use up the oxygen faster than it can be replenished through the water surface. When loadings are such that oxygen concentrations sag to particular levels, e.g. 4 ppm, the more sensitive fish are driven out or are excluded from such reaches. There is an approximate threshold effect, related to a discontinuity of response to intensifying loadings, that has long been used for setting limits on loadings of such materials into flowing waters. Such a limit is sometimes called an "assimilative capacity" which has come to be a euphemism for the corresponding level of waste loading or pollution that will nevertheless cause harm but only (in theory) to acceptable limits.

Gravel and rock extraction

In some parts of the Great Lakes, the continental glaciers left behind deposits of boulders, the glacial erratics formed into reefs of reworked drumlins, etc. Some of these served as nearshore or offshore spawning reefs for lake trout, lake whitefish, and other species.

Deposits of rocks and gravel near metropolitan areas, as around Toronto, were mined for construction material beginning over a century ago. The direct impacts on the local fish stocks and the fish community were apparently never studied in the Great Lakes, in contrast with those of some other contemporaneous cultural stresses such as loadings by organics. Circumstantial historical evidence (Whillans 1979) suggests that some spawning stocks that frequented such reefs were extinguished, presumably when the character of the reef became so altered as to have lost the features that are particularly important for spawning success. Perhaps studies currently underway elsewhere on the effects of such mineral extractions may provide evidence of the mechanism underlying this discontinuity.

Why is Disequilibrium Surprising?

In summary of the above examples, we infer that discontinuities in the functional response of fish communities to intensifying stress may well have occurred for each of the cultural stresses that were allowed to become quite intensive. In cases where a threshold has been quantified in approximate terms, such information has been used to set regulations in an attempt to prevent the catastrophic transformation of some valued feature of the Great Lakes. The approach has been largely unsuccessful, however, because not all cultural stresses were controlled effectively and because little attention was directed to the synergisms that occurred between stresses. Unacceptable combined effects could occur even though individual stress thresholds may not have been exceeded. Little scientific attention has yet been directed to the issue of discontinuities and "surprises" in the complex response function to interacting cultural stresses.

As the cultural stresses are being relaxed or mitigated progressively in the Great Lakes, recovery sequences are becoming apparent. Presumably these will also exhibit recovery discontinuities, but likely not at the levels of stress at which degradative discontinuities occurred. There will likely be some "overshoot" with a "hysteresis" effect. Our inability to predict these discontinuities, even through detailed analysis of individual fish stocks and cultural stresses, has prompted efforts to modify our approach to that of ecosystem management.

The systemic "science of surprise" and related adaptive management methods under development by Holling and colleagues (Holling 1978; ESSA 1982; Regier 1985) seem to be particularly relevant to these perspectives on ecological nature. Interpreted in a somewhat extreme way, Holling's concepts of surprise start from the general inference that long-term equilibrium or steady-state conditions are quite unusual in present-day ecosystems, especially in those that are strongly influenced by humans. Change is now ubiquitous, apparently in many aspects important to humans, not infrequently in the form of dramatic transformations that occur over relatively short time intervals.

In recent years, Holling (1986) has become interested in disequilibria on geographic scales from regional to global, and temporal scales from decades to centuries. Our paper deals with ecological and human-nature disequilibria of local and regional scale (from a bay of a Great Lake to the Great Lakes Basin) and of time constraints in the scale of years and decades; the concepts may be extendable to nonaquatic systems (see Rapport et al. 1985) and may provide analogues (or homologues?) for phenomena of larger scale (see Regier and Baskerville 1986).

So much of quantitative fisheries theory concerning both ecological and economic fisheries phenomena starts from a preconception that natural processes, human culture, and interactions of nature and culture are all in a state approaching that of a "stable equilibrium." Apparently we have learned the steady-state theory not so much as a gross oversimplification, nor as following from imaginary axioms from which to create mathematical theorems, but more as a characterization of an ideal state to which both nature and humans should aspire. It is a challenge of ecosystem science to deal with nonequilibrium "aberrations" seriously in their own right as intrinsic attributes of natural systems.

Rehabilitation of Degraded Ecosystems

In this section we outline a minimally sufficient set of components for ecosystem science in the Great Lakes region, consistent with the ecological perspectives sketched above.

'Ecosystem rehabilitation" may be defined based on a number of strategies of ecosystem management (see Francis et al. 1979): *degradation* refers to any human activity that alters an ecosystem in a way that is inimicable to our values of nature and natural systems; *restoration* refers to attempts to restore both biotic and abiotic features of a degraded ecosystem to their natural states; *enhancement* refers to attempts to introduce desirable features or enhance desirable aspects of an ecosystem, without reference to the original, natural state of the ecosystem; *remediation* refers to discontinuation of past abusive practices, and may involve discontinuation of harmful loadings or removal of sediments and dumps of hazardous materials; *mitigation* refers to the use of artificial or surrogate ecosystem components to replace lost or degraded natural ecosystem components, especially with regard to plant and animal species and structural features of habitats; and *rehabilitation* is a pragmatic mix of restoration, enhancement, remediation, mitigation, and nondegradation to benefit highly valued, sensitive uses of the ecosystem.

Ecological Information Network

Some essential features and elements of an ecological information network that would be capable of addressing ecosystem rehabilitation in the above context may be expanded from those proposed by Regier and Rapport (1983) as follows:

concepts and methods of appropriate spatial and temporal scope, and appropriate scale and detail; scientific concepts of "surprise" and management methods of "adaptation to surprise" (e.g.) Holling 1978, 1986); an information set that includes maps of spatial ecosystemic features, time series of diagnostic ecological features, models of relational/causal processes, assessments of proposed management interventions, and management case studies; holistically, adequate comprehension of the ecosystem's evolutionary/successional processes, responsiveness/adaptiveness to external factors, and recovery sequences after relaxation of external stress; analytically, sufficient specification of causal links within the ecosystem with respect to internal effects due to external natural processes and components, internal natural processes and components, and ecosystem man–nature interactions; strategic management objectives that reach appropriate social compromises with respect to material well-being/progress, cultural opportunities/equity, environmental harmony/ethics, and management costs; and tactical management considerations that include the value and relevance of long-term monitoring data, of data that relate to recurring or unsolved problems, of data relevant to the governance of major interest groups that use features of the ecosystem, and of data that integrate aspects of ecosystem health.

In practice, such a protocol of "elements" is not as useful for deducing specifically what kind of data should be collected for purposes of ecosystem rehabilitation as it is for assessing proposed or existing information sets as to their completeness.

Analysis, Design, and Holistic Ecosystem Husbandry

Applied ecology has various fields depending on the degree and intensity of control exercised by the users or managers of the productive system. At one extreme with regard to aquatic systems is the management involved with self-reproducing and self-regulating wild fish stocks in an ecosystem modified relatively little by humans. Here, maximum sustainable yield (MSY) of a few of the most preferred species may be the management objective, perhaps on the implicit condition that MSY be defined so as not to trigger any major disequilibrium in the natural system.

The ecological constraints on MSY are seldom stated explicitly – they usually lie submerged in informal conventions shared by researchers, managers, fishermen, etc. The science developed for such fisheries is largely analytical: natural mortality rates, stock recruitment relationships, organismal growth rates, etc., are estimated. The resulting estimates are then assembled into some aggregated form to yield an estimate of MSY, but without clear specification of what that estimate of MSY means in the context of the fish community or the aquatic ecosystem. This kind of fisheries science has been dominant for half a century now in the Great Lakes and in oceanic fisheries of the Northern Hemisphere (Larkin 1977).

At another extreme of fisheries science lies aquaculture of many varieties. Here the aquatic system is under quite close control of the manager, and the species being cultured is usually domesticated or "man-made" to some extent. The kind of science most relevant here is not conventional analysis but a subsequent stage in which the objectives of the manager are explicitly specified and the scientific information is used to design some approximately optimal procedures of achieving the objectives. Science is then used to monitor the process to permit correction of deviations from the designed process.

In the Great Lakes, as also in numerous large river and nearshore oceanic fisheries, we are now in a state intermediate between the kind of science appropriate to conservative intervention in relatively unstressed wild ecosystems and the kind of science appropriate for the design and control of intensive culture systems. We call this more holistic intermediate stage, in which analysis and design are now about equally important, ecosystem husbandry if the ecosystem is relatively healthy and productive of high quality resources, or ecosystem therapy or rehabilitation when the ecosystem is so degraded as to be relatively unproductive of valued resources.

The Symposium on Salmonid Communities in Oligotrophic Lakes (Regier and Loftus 1972) was an early event in the development of a science in which analysis, holistic study, and design were balanced, although the design aspect (e.g. as reflected in the introductions of Pacific salmons) was not as explicit as was the analytical aspect. With the Great Lakes Ecosystem Rehabilitation studies (Francis et al. 1979) the holistic and design emphases became clearer and were linked explicitly to the goals specified in the 1954 Great Lakes Fisheries Convention and in the 1972 and 1978 Great Lakes Water Quality Agreements.

Resource Allocation: Hard Shell, Soft Core

To be relevant and successful in implementing the foregoing ideas, ecosystem science must seek to understand interactions of the ecological, social, economic, and political subsystems of the human–nature ecosystem. Such interactions influence the ways in which society allocates rights and responsibilities pertaining to ecological resources, and consequently determine to a large extent the fate of those resources. This is a recurring theme in discussions of ecosystem management (Karr et al. 1985; Barrett 1985; Risser 1985), reflecting its importance as well as the theoretical and practical difficulties involved. The study of resource allocation mechanisms may provide powerful insights into the interactions of nature and culture.

Rights to the use of various ecological resources may be classified along gradients of exclusive (owned by a person or group of people) to nonexclusive ("public property") and of transferable (can be bartered or sold) to nontransferable (can be administered, but not bartered or sold) (see figure in Regier and Grima 1985, p. 853, based on Dales 1975). The four extremes of this two-dimensional classification may all appear in a centralized, hierarchical system where "hard" methods, or clear and sharply defined power relationships, formality, explicit accountability, hierarchy, and social competition and predation, prevail.

Hard methods may serve best when a conflict between powerful forces reaches a stage where the more powerful instruments and agencies of society are called into action to resolve it. This occurs when a conflict may lead to serious criminal activity, as when two competing groups of fishermen resort to direct personal violence and property destruction, or when contamination of water and consequently of fish by a chemical company leads to a loss of income for fishermen and a health threat to consumers of fish. Resolution of the conflict may involve clarification of rights as in creation of an institutution (e.g. a tribunal or a free market) to ensure proper exercise of the rights and related responsibilities. The dominant tendency in fisheries science as related to maximum sustained yield and/or maximum economic yield has long been toward compatability of the ecological and economic science with

"hard" systems of resource allocation (Regier and Grima 1985). Hard methods are also commonly used to manage large point sources of pollution that degrade water quality and large users that diminish water quantity in the Great Lakes.

But when the more extreme forms of conflict are resolved, many less extreme local difficulties may persist for which the "hard methods" are inefficient, at best. Here the "softer" methods may apply (Francis et al. 1985; Devall and Sessions 1984), where allocation of resource rights may be less formal, less structured, and less hierarchical, as in the natural resource husbandry of a noncentralized, more cooperative hinterland, or in community level education and "peer pressure" mechanisms to improve land use practices related to non-point-source pollutants such as phosphorus from land runoff. The development of community-level negotiation and semiformal market systems as allocative devices for ecological resources entrains a need for relevant, "softer" ecosystem science.

Conclusion

Initial rehabilitative research and practice in the Great Lakes have tended to focus on certain areas (often bays) that are severely degraded, or are perceived to be "environmentally sensitive areas" and are in danger of severe degradation. These areas include Green Bay on Lake Michigan (Harris et al. 1982), Long Point Bay on Lake Erie (Francis et al. 1985), and Toronto and Hamilton Harbours on Lake Ontario (Whillans 1979; Holmes and Whillans 1984; Holmes 1986). Of these, all but Long Point Bay are now severely degraded although showing some signs of rehabilitative progress, and have been designated "areas of concern" (IJC/WQB 1985).

These areas and many others not officially recognized are or have been important ecological "centres of organization," not least in that they contained spawning, rearing, and feeding habitat for a wide variety of desirable fish species. The characteristics that make these areas biologically important (sheltered waters and access to river mouths in particular) also make them centres of cultural organization, as harbours and centres of trade. With few exceptions, human use of these areas as it is currently practised – think especially of shoreline structuring, waste disposal, and navigation – is generally incompatible with healthy, productive, sustainable aquatic ecosystems.

Under the 1978 Great Lakes Water Quality Agreement, governmental agencies in Canada and the United States have agreed to develop "remedial action plans" for each of 42 "areas of concern." The mix of science and practice for effective rehabilitation of such areas will need to be site specific, depending on ecological, economic, and political considerations. It will require appropriate "holistic" ecological foresight, planning flexibility, and spatial perspective ("design") as well as detailed understanding of certain ecological processes ("analysis"). "Soft methods" of allocating resources and responsibility will be needed to complement the "hard methods" which will, at best, only cope with the more serious issues.

Heretofore, ecosystem science has been developed mostly to serve hard methods of resource allocation and ecosystem management conflict resolution. In this paper (see also Regier and Henderson 1973) we have sketched an approach that would serve the soft methods more directly.

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Interactions in North-Temperate Lake Fish Communities

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Several species interrelationships influenced by actural or preceived disturbances were described which managers should consider when manipulating fish populations and communities. For example, factors controlling homeostasis of adult northern pike (*Esox lucius*) and white suckers (*Catostomus commersoni*) in northern lakes may still operate despite walleye reductions, suggesting less niche overlap than we previously expected. In more northern centrarchid type communities, percid abundance and condition depend on how well northern pike and other predators control both white sucker and bluegill (*Lepomis macrochirus*) abundance. Evidence from walleye (*Stizostedion vitreum vitreum*) fry and fingerling plantings suggest that when intense interactions between species determine their abundance, these interactions occur during the very early life stages. Climatic changes may also be influential in determining abundance of several fish species common in north-temperate lakes. Rehabilitation of preferred species by removal of less desirable fishes can be successful in some ecosystems, but we warn that an undesirable compensatory response may also occur.

On a décrit plusieurs relations interspécifiques modifiées par des perturbations, réelles ou perçues, que devaient prendre en considération les gestionnaires au cours de la transformation de populations et de communautés de poissons. Ainsi, les facteurs régissant l'homéostasie des adultes du grand brochet (*Esox lucius*) et du meunier noir (*Catostomus commersoni*) dans les lacs du nord peuvent toujours s'appliquer en dépit d'un déclin des populations de dorés jaunes (*Stizostedion vitreum vitreum*), ce qui porte à croire à un moins grand recouvrement des niches que l'on ne l'avait prévu. Chez les communautés du type centrarchidés situées plus au nord, l'abondance et la condition des percidés sont fonction de la façon dont le grand brochet et d'autres prédateurs limitent l'abondance du meunier noir et du crapet arlequin (*Lepomis macrochirus*). Les résultats de l'ensemencement de plans d'eau par des alevins et de très jeunes dorés jaunes portent à croire que lorsque des interactions intenses entre espèces en déterminent l'abondance, ces interactions agissent très tôt au cours du cycle vital. Des modifications climatiques peuvent aussi agir sur l'abondance de plusieurs espèces de poisson communes dans les lacs de la zone septentrionale tempérée. Le rétablissement d'espèces souhaitées par l'élimination d'espèces moins intéressantes peut être réussi dans certains écosystèmes, mais les auteurs soulignent qu'il peut y avoir une réponse compensatoire non souhaitée.

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Fishery managers need better criteria for more precisely predicting the outcome of a given management activity. Theoretical concepts, although useful in a more global context, do not provide the resolution necessary for more specific or local situations. The development of better criteria requires that we improve our understanding of species interactions and the mechanisms that control them.

There has been considerable progress in this area. Recent symposia have increased our understanding of how changes in species abundance are brought about by exploitation, species introductions, and eutrophication in salmonid (Loftus and Regier 1972) and percid communities (Colby and Wigmore 1977). Also, we now have a better understanding of other broad external influences which affect species dominance and succession such as changes in lake acidity (Rahel and Magnuson 1983) and climate (Inskip and Magnuson 1983).

However, our ability to predict is less certain when systems are lightly or moderately disturbed as happens, for example, after changing fishery regulations or evoking strategies to rehabilitate fisheries or fish habitat. We feel one approach to improve our understanding of species interaction is to compile and analyze more case histories of disturbed fisheries to improve our understanding of community dynamics.

Our approach has been to survey the past management initiatives in order to identify factors affecting species abundance and to identify mechanisms controlling important species interactions. For example, we have summarized a number of case histories for lakes in which particular species have been

introduced, or their numbers have been augmented by stocking, or decreased by deliberate removals, or in which habitat has been altered. Although these studies were not controlled, we attribute the dynamics of the fish populations to the manipulations applied. Minimally, such case histories describe the types of events which can occur in given situations — defining an array of possible system behaviors in terms of the dynamics of major species. We have used a graphical approach (phase diagrams, Holling 1973) to summarize the relationships between the abundances of particular species over time for a subset of the case histories. Important interactions, mechanisms, or behaviors are identified as various data sets are reviewed.

Natural Influences on Species Interactions

Abiotic factors (e.g. lakes as morphoedaphic templates, Steedman and Regier 1987) determine the type (biochemical nature of matter or species composition) and rate (energy availability) of biological production processes. Abiotic variables such as temperature and light regimes can have profound effects on the physiology of fishes and subsequently their population demographics. Within abiotic constraints, many specific interactions are determined by biological processes, i.e. competition and predation. Temperature, for instance, affects mortality through its influence on predator activity and maximum ration (Crowder et al. 1987). Consequently, changes in weather and climate may have a profound and overriding influence on species interactions.

Effect of Weather and Climate on Species Abundance

Several authors have shown that smallmouth bass (*Micropterus dolomieui*) reproduction and year class strength is enhanced by warm summer temperatures (Fry and Watt 1957; Christie 1957; Forney 1972; Shuter et al. 1980; Serns 1982b). Temperature and other abiotic factors such as wind conditions and regularity of spring warming appear to be important in the recruitment of a variety of smaller inland and Great Lakes fishes including lake whitefish (*Coregonus clupeaformis*) (Taylor et al. 1987; Christie and Regier 1973), yellow perch (*Perca flavescens*) (Clady 1967), walleye (*Stizostedion vitreum vitreum*) (Busch et al. 1975; Chevalier 1977; Serns 1982a), alewife (*Alosa pseudoharengus*) (O'Gorman et al. 1987), and cisco (*Coregonus artedii*) (Hartman 1973). Following a particular mix of weather conditions in a series of years, behavioral or numerical dominance of one species relative to others may change rapidly.

In many of the studies cited above, it was unknown whether low temperatures were direct sources of mortality or whether they caused a reduction in recruitment indirectly through biotic interactions. After smallmouth bass were introduced into four Minnesota lakes between 1945 and 1948, walleye populations declined, and smallmouth populations increased through the mid- to late 1950's and early 1960's (Johnson and Hale 1977). A similar trend was noted in the native smallmouth bass and walleye populations in Big Pine Lake, Wisconsin, over the same period and was attributed to climatic trends rather than competitive interactions between the species (Inskip and Magnuson 1983).

Cisco Ecology

The cisco is an important prey species for northern pike and walleye in coolwater fish communities (Ryder and Kerr 1978; Colby et al. 1979) and for lake trout (*Salvelinus namaycush*) in coldwater communities (Martin and Olver 1980). Northern pike, walleye, and lake trout are size-selective predators (Popova 1982; Parsons 1971; Martin and Olver 1980). Although they may consume prey of a wide range of size, the maximum and average size of prey consumed increases with predator size.

The rate of growth of ciscoes is therefore one factor which affects their vulnerability to size-selective predators. There is a wide range in cisco growth rates and the maximum size attained between lakes, as reviewed for Saskatchewan (Rawson 1957; Ruggles 1959; Atton and Johnson 1962; Koshinsky 1964), Alberta (Paetz and Zelt 1974), and northern Ontario (Fig. 1). A measure of how closely coupled a cisco–predator relationship is in a given lake could be described relatively through a measure of how long cisco remain within a size range vulnerable to

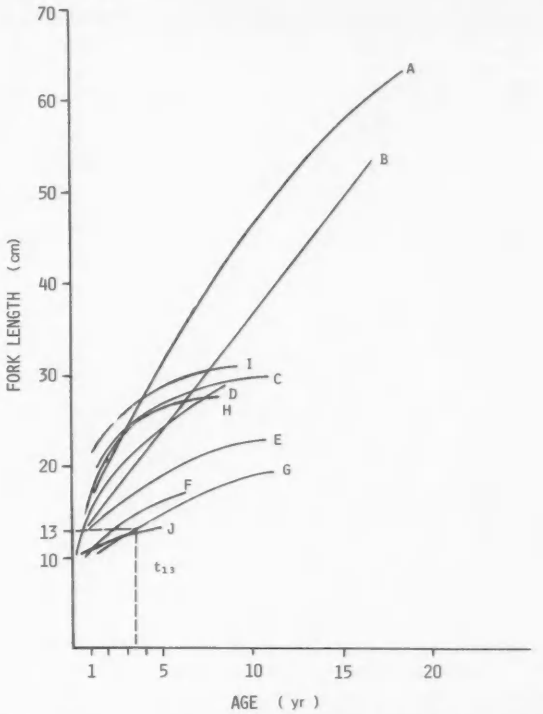

FIG. 1. Size at age for cisco populations sampled from eight north-central and two eastern Ontario lakes using gill nets (see sources of information on cisco growth). The curves were drawn by eye. The t_{13} values were estimted by von Bertalanffy growth models of portions of the growth data or by direct observation as the time (years) to reach 13 cm FL. Negative values were assigned a value of 0.5 yr. The t_{13} FL value corresponds to the size of the largest fish consumed by 39 cm TL walleye in Lake Erie (Parsons 1971) and is used as our definition of the upper size of prey vulnerable to intermediate-sized walleye. Values of t_{13} and method of aging (parentheses) for each lakes follows: A = Shebandowan Lake (t_{13} = 0.5 fin rays); B = Greenwater Lake (t_{13} = 1.2, fin rays/otoliths); C = Crooked Pine Lake (t_{13} = 0.5, scales/otoliths); D = Lac des Mille Laes (t_{13} = 0.3, scales otoliths); E = Pickerel Lake (t_{13} = 0.9, otoliths); F = Muskeg Lake (t_{13} = 2.3, otoliths); G = Pekagoning Lake (t_{13} = 3.2, otoliths); H = Twelvemile Lake (t_{13} = 0.8, scales); I = Drag Lake (t_{13} = <1, scales); J = Bernadine Lake (t_{13} = 4.3, otoliths).

predation. Parsons (1971) found that larger walleye (greater than 39 cm) consumed fish prey ranging in size between 10 and 14 cm total length (TL) in Lake Erie. Mosindy (1981) found that the largest cisco consumed by walleye in Savanne Lake were 14 cm in length. Using this upper size limit of 14 cm TL or 13 cm fork length (FL), we define t_{13} as the time period during which a cohort of cisco is vulnerable to predation (Fig. 1). This sample of Ontario lakes indicates a range of t_{13} values of 0.3–4.3 yr.

Lac des Mille Lacs provides an example of how the lack of suitably sized prey fish may affect the growth rate of a predator such as walleye (P. A. Ryan, unpubl. data; see Elsey and Thompson 1977 for a description of the lake). The growth increments exhibited by walleye decline with increasing age and fish size until age 5 and size 36 cm, after which walleye grow rapidly again (Fig. 2). Yellow perch are the most important food item numerically in the diet of small and intermediate sized walleye in Lac des Mille Lacs (Fig. 3A, 3B). Over the size range 35–40 cm, however, the walleye diet changes to include more sticklebacks and, from this size and up, a steadily increasing number of coregonids (primarily cisco). There is also a change in the average size of fish prey consumed although this change is over the interval 40–45 cm. Mosindy (1981) found a similar pattern in walleye diets in nearby Savanne Lake where cisco only occurred in the diets of walleye larger than 40 cm TL and occurrence increased with walleye size.

In contrast with the Lac des Mille Lacs data, Parsons (1971) found a steady increase in the size of fish prey used by walleye in Lake Erie and the growth pattern was relatively linear. The change in prey size and diet of walleye in Lac des Mille Lacs does not correspond exactly with the change in walleye growth pattern, but we ascribe this to the time of year of the diet study. In addition, the use of numeric composition and average prey length undervalues the contribution of cisco to the diet. The cisco of Lac des Mille Lacs exhibited extremely rapid growth ($t_{13} = 0.3$ yr) and would only have been vulnerable to the 35–40 cm walleye earlier in the year.

The growth increment plot (Fig. 2) is analogous to a *K*-line description of growth (Paloheimo and Dickie 1966). The change in growth pattern is essentially a transition between *K*-lines which are characteristic of forage types (Kerr and Ryder 1977). It is apparent that if the growth rate of cisco was slower in Lac des Mille Lacs, cisco would be available as prey for smaller walleye and improve the growth rate of intermediate-sized walleye with consequent effects on production and average size of fish in the sport fishery.

The introduction of cisco into Lake Opeongo (Martin 1970) led to an increase in the sport fish harvest of lake trout, but had both positive and negative effects on the trout population. The growth rate of young trout was reduced and maturity was delayed. Older trout exhibited an increase in growth rate and fecundity. The reduced growth rate of young trout was attributed to a reduction in the abundance of young-of-the-year (YOY) yellow perch following the introduction of cisco. A comparative analysis of growth rates of lake trout in central Ontario lakes suggested that slower growth was associated with higher abundance of cisco (Ontario Ministry of Natural Resources (OMNR) 1984).

The explanation of changed lake trout growth patterns in Lake Opeongo may not apply to other lakes directly. The invertebrate fauna of Lake Opeongo lacks some important glacial relict species (*Mysis relicta, Ponteporeia hoyi*; Martin and Chapman 1965) which are important in lake trout diets elsewhere (Martin and Olver 1980; Black 1980). It is likely that

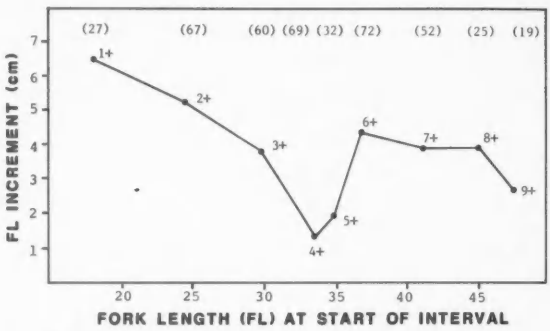

FIG. 2. Mean growth increments of Lac des Mille Lacs walleye (sexes combined) as determined from size at age obsevations made during the fall of 1983 (P. Ryan, unpubl. data). Sample sizes in parentheses.

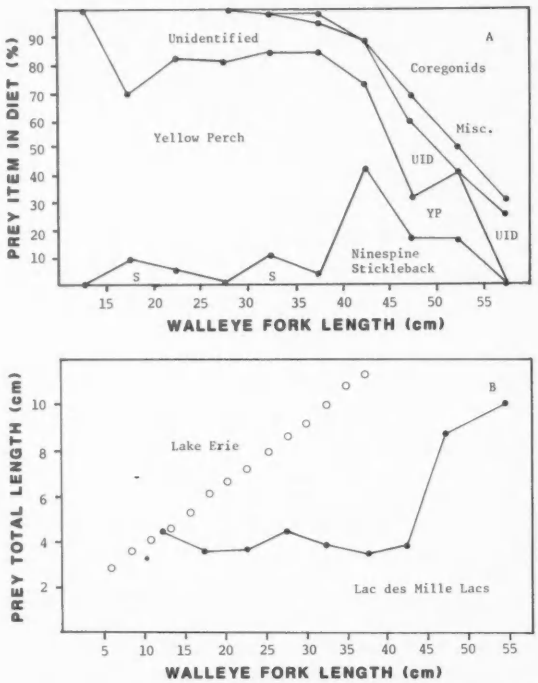

FIG. 3. Relative abundance and length of prey fish in the diet of Lac des Mille Lacs walleye in fall 1983 (September–October) (P. Ryan, unpubl. data). (A) Numeric composition of prey fish in relation to size of walleye (5 cm FL size classes). The miscellaneous category includes burbot (*Lota lota*) and white sucker. (B) Relationship between the mean size of prey fish (without reconstruction) and size of walleye (5 cm FL size classes of walleye length). The reference line (open circles) is for fish prey size versus walleye length in Lake Erie, based on original prey size (Parsons 1971).

the correlation of slow trout growth with high cisco abundance is usually based on competition for common forage items such as *M. relicta* and *P. hoyi*, which are important in the diet of both young lake trout and large cisco (Scott and Crossman 1973; Martin and Olver 1980; Black 1980).

There are a number of ecological relationships which may interact together to control the trophic relationships between

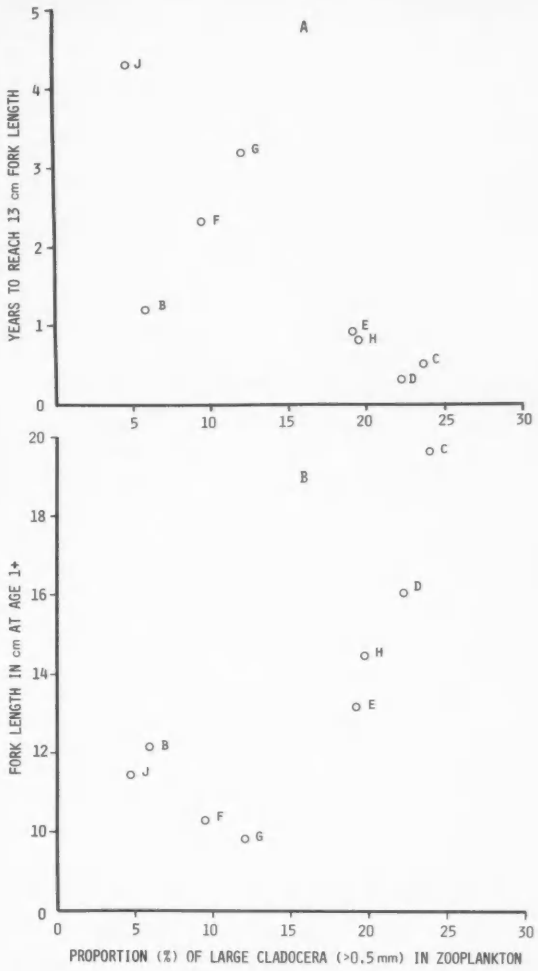

FIG. 4. Relationship between proportion of large cladocerans (>0.5 mm) in zooplankton and (A) years required to reach a fork length of 13 cm (t_{13} in Fig. 1) and (B) size at age 1 estimated from von Bertalanffy growth equations or direct observations. Alphabetical codes for lakes are the same as in Fig. 1. In Fig. 4A, $r = -0.762$ df = 6, and $P \leq 0.05$ and $r = -0.937$, df = 5, and $P \leq 0.01$ when Greenwater Lake (B) is excluded. In Fig. 4B, $r = -0.791$ df = 6, and $P \leq 0.05$ and $r = -0.827$ df = 5, and $P \leq 0.01$ when Greenwater Lake is excluded.

zooplankton, *Mysis*, cisco, and lake trout. From the top down, we expect that the growth rate of cisco affects their vulnerability to predation by trout, as described for walleye earlier. The growth rate of cisco in early life should be related to the abundance and suitability of zooplankton forage. We could not examine abundance of zooplankton, but did find that the growth rate of cisco was related to zooplankton quality (Fig. 4). Planktivorous fish actively select large cladocerans when foraging, to an extent where they have changed the zooplankton fauna of lakes (Zaret 1980). The growth rate of cisco in northwestern Ontario lakes exhibited a strong positive correlation with the percentage of large cladocerans (> 0.5 mm) in zooplankton samples.

Mysis relicta is an important invertebrate predator of zooplankton and can regulate its taxonomic composition to the extent that favoured prey types such as large cladocerans become rare following *Mysis* introductions (Goldman 1981; Kinsten and Olsen 1981; Lasenby et al. 1986). In the absence of intense fish predation, larger cladoceran forms are common in the plankton because of their relatively lower vulnerability to smaller invertebrate (zooplankton) predators (Zaret 1980).

If these factors are considered as vectors, their directions suggest that this simple food web should probably tend toward one of two states (Fig. 5). One state would be characterized by abundant lake trout and mysids, a zooplankton fauna composed of small taxa, and a cisco population in which the individuals grow slowly. There is evidence that this state has been achieved in Swedish lakes following *Mysis* introduction (Furst et al. 1986). In their review of effects on the fish community, these investigators also found instances where the growth rate of young lake trout improved, and benthic feeding coregonids benefited from *Mysis* introductions. Pelagic populations of Arctic char (*Salvelinus alpinus*) and coregonids which normally fed on cladocerans failed to switch to *Mysis* and declined in numbers.

The alternative state would be characterized by a small population of lake trout and low abundance of mysids, a zooplankton fauna containing larger species of cladocerans, and a large cisco population in which individuals exhibit fast growth and large asymptotic size. This state would be achieved by increasing fish predation on *Mysis* to a level such that the composition of the zooplankton is no longer regulated by *Mysis* predation. A reduction in the abundance of top predators such as larger lake trout, walleye, and northern pike would permit cisco to increase in abundance. The abundance of other predators of *Mysis* (e.g. sculpins and cisco) would also increase when the abundance of large lake trout was reduced.

This state may not be stable, since cisco could conceivably overgraze the zooplankton and cause changes in the faunal composition. An environmental constraint on cisco reproduction could ensure maintenance of the second food web state by maintaining cisco populations at levels too low to overgraze and change the composition of the zooplankton. In northern reservoir lakes, fall-spawning coregonids may be adversely affected by overwinter drawdown, as eggs that are deposited in shallow water may be desiccated with relatively minimal water level changes (Gaboury and Patalas 1984). There is some indication that winter drawdown has affected cisco recruitment in Shebandowan Lake (5909 ha; Wepruk 1983; L. Godwin, pers. comm.). The growth of cisco in Shebandowan Lake is rapid and it appears that the asymptotic size is much larger than the largest (60+ cm) cisco observed. Also, the size at age of walleye has been declining for many years (Wepruk 1983).

Species Interactions due to Human Disturbances

Both addition or removal of a species in a fish community or habitat alteration can have a profound effect on community homeostasis and the manner in which energy and biomass is transported through the community. Thus, by viewing certain management initiatives of the past as manipulative experiments, we can make generalizations regarding species interactions.

Disturbances due to Species Additions

Rainbow smelt introductions

Frequently, predator or prey species gain access or are added

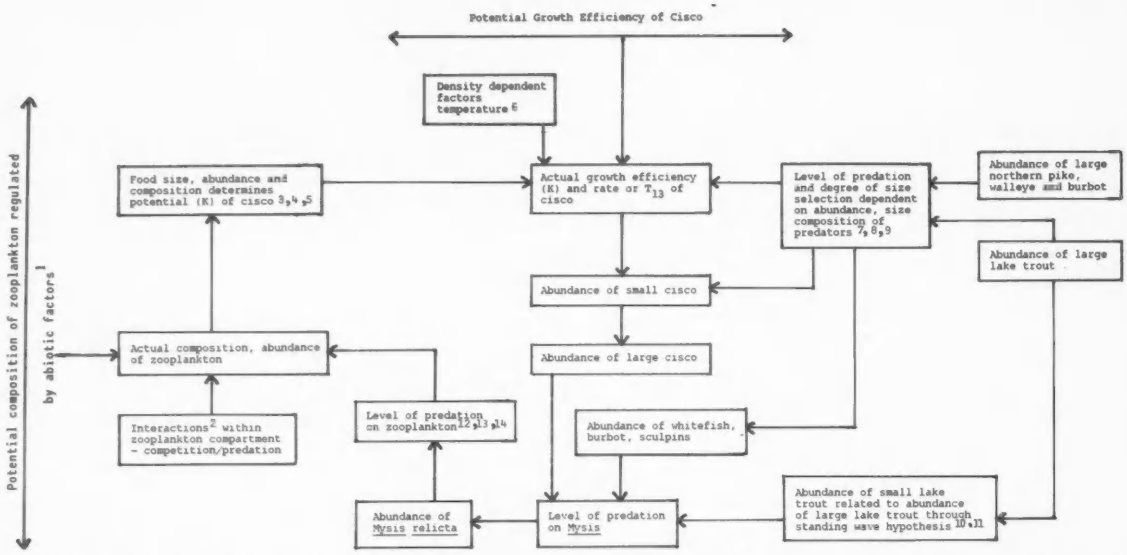

FIG. 5. Model of trophic relationships for a coldwater food web in a north-temperate lake with a focus on effects of size-selective predation. The predation relationships are summarized from Rawson (1951), Dryer et al. (1965), L. Johnson (1975), and Scott and Crossman (1973). References for compartments are (1) Patalas 1971; (2) Zaret 1980; (3) Paloheimo and Dickie 1966; (4) Kerr and Martin 1970; (5) Kerr 1971; (6) Weatherley 1972; (7) Popova 1982; (8) Parsons 1971; (9) Martin and Olver 1980; (10) Johnson 1972; (11) Johnson 1973; (12) Goldman 1981; (13) Kinsten and Olsen 1981; (14) Lasenby et al. 1986.

to inland lakes to enhance fishing. The risks involved in fishery enhancement, however, are not always anticipated. One of the more notorious introductions in the Great Lakes and surrounding area has been the rainbow smelt (*Osmerus mordax*).

Rainbow smelt are facultative piscivores in the Great Lakes, sometimes consuming substantial quantitites of small fish (Gordon 1961). An increase in abundance of smelt and the concomitant decline of cisco in the Minnesota waters of Lake Superior were described by Anderson and Smith (1971) and illustrated in Ryder and Edwards (1985). Smith (1972) reported that there have been several instances of decreases in abundance of cisco as smelt increased. This relationship occurred twice each in Lakes Michigan and Huron and has also occurred in Lake Superior.

Selgeby et al. (1978) examined the feeding habits of rainbow smelt following the spring hatch of cisco in Black Bay, Lake Superior, and found an average of 35.8 cisco larvae/stomach of adult smelt (>100 mm). Despite these findings, the authors felt that smelt predation did not reduce the harvestable population because the Black Bay commercial cisco fishery was at historically high catch levels. In the Apostle Islands region, densities of smelt and cisco larvae were much lower than in Black Bay and no smelt were found to have eaten cisco larvae. Selgeby et al. (1978) concluded that predation by smelt on cisco larvae was not a major factor suppressing cisco populations in either Black Bay or the the Apostle Islands region.

In contrast, Swenson (1978) believed that turbidity due to erosion of glacial lacustrine red clays may have restricted the feeding zone of cisco and smelt in Wisconsin waters and made cisco larvae more vulnerable to smelt predation. Swenson (1978) suggested that although no cisco larvae were found in smelt diets, the probability of detection was low because larval cisco were rare at the time in western Lake Superior.

In large lakes, such as Lake Champlain, New York (114 046 ha), spatial segregation may reduce the intensity of interactions. This lake consists of two large basins. Adult walleye and smelt spawn mainly in the south basin and then migrate back to the north basin. Walleye larvae develop in the south basin and do not move into the north basin until later in life (likely as subadults). Biologists (A. Schiavone Jr., Fish. Biol., Dep. Environ. Conserv., Watertown, NY, pers. comm.) believe that good natural reproduction of both walleye and smelt in this large lake may be due to the spatial segregation of adult smelt from larval walleye. Unlike smelt and cisco which occupy similar thermal regimes, adult smelt and larval walleye are likely to be both spatially and thermally segregated.

Rainbow smelt also prey on young bloaters (*Coregonus hoyi*) in Lake Michigan (Stedman and Argyle 1985). These authors cautioned that although smelt predation appears not to have affected bloater populations appreciably in recent years, it may have the potential to do so in the future. Also, Brandt and Madon (1986) found that rainbow smelt feed on small slimy sculpin (*Coltus cognatus*) (12.7–21.1 mm) in Lake Ontario and suggested that rainbow smelt may compete with juvenile lake trout for slimy sculpin in the Great Lakes.

More recent observations in small inland lakes (400–600 ha) justify the warning by Stedman and Argyle (1985) and Brandt and Madon (1986) that rainbow smelt can have a negative influence on endemic species (Tables 1 and 2). Lake whitefish populations are experiencing recruitment failure in Twelvemile and Elliott lakes, Ontario, where only large old whitefish are present (Loftus and Hulsman 1986; K. Armstrong, pers. comm.). Smelt have been observed to feed heavily on coregonid larvae in Twelvemile Lake (Loftus and Hulsman 1986), and this, plus possibly some competition, may be the cause of the apparent demise of whitefish. Smelt are also present in other central Ontario lakes. In two lakes (Lake Simcoe and Elliot Lake), lake whitefish recruitment and yields appear to be

inversely related to smelt abundance. Loftus and Hulsman (1986), citing Warner and Fenderson (1963), pointed out that in eight of Maine's Fish River Lakes which once supported good lake whitefish populations, seven lakes stocked with smelt in the 1890's now only support residual populations of whitefish. In Lake Lucerne, Wisconsin, the whitefish population declined dramatically and eventually collapsed after the invasion and increase of smelt (Tables 1 and 2).

As further examples of the negative effect of rainbow smelt, their introduction in two Wisconsin lakes (Lucerne and Fence) was associated with drastic declines in walleye reproduction or recruitment (Table 1). Hartman (1973) also reported that smelt may have had an adverse impact on walleye in Lake Erie. However, fingerling walleye were successfully stocked in Lake Lucerne, suggesting that they were too big to be eaten.

Lake Lucerne historically was dominated by walleye as the top predator. In recent years, however, this dominance has shifted from walleye to smallmouth bass. Natural reproduction of walleye in Lake Lucerne has been poor for about the last 10 yr, following smelt introduction, with none occurring in the last 3 yr, so far as could be determined through fall electrofishing surveys. Fingerlings stocked in 1982 and 1983 have apparently survived well and were well represented in an electrofishing survey in September 1983 and a gillnet survey in 1985, indicating that if smelt are having an adverse effect on walleye, it is likely earlier during the egg or fry stages.

The introduction of rainbow smelt appears to have a negative influence on many endemic species, especially in the smaller inland lakes (Table 2). The negative association of rainbow smelt and cisco is common in large inland lakes such as the Laurentian Great Lakes. Similar negative relationships between European smelt (*Osmerus eperlanus*) and coregonids have been reported in the Soviet literature (Reshetnikov 1979). Because of their frequency, the negative interaction between smelt and cisco seems more than coincidental and probably is due in part to their pelagic niche overlap.

Spatial, thermal, and temporal segregation may reduce the intensity of association between rainbow smelt and other endemic species, especially if their abundance is not too great. For example, there are even thriving whitefish fisheries in the Great Lakes where smelt are abundant and walleye do not appear to be negatively influenced in Lake Champlain, New York, where spatial and possibly thermal and temporal segregation reduce the intensity of interactions. The fact that walleye fingerling plantings survive in lakes containing rainbow smelt suggests that the negative effect of smelt on walleye occurs very early in the latter's life history.

Evidence of smelt predation on coregonid larvae in several inland lakes supports the hypothesis of smelt having a negative influence on cisco in Lakes Michigan, Huron, and Superior. Some inland lake case histories suggest also that smelt can have a negative influence on whitefish and walleye, which may explain the whitefish and walleye recoveries in Lake Michigan in the late 1940's following the 1942–43 smelt die-off in the Great Lakes.

Northern pike introductions

The introduction of northern pike through stocking in two small central Minnesota lakes, Horseshoe and Grace, greatly altered their fish communities (Anderson and Schupp 1986; Wesloh and Olson 1962). In both lakes, declines in yellow perch abundance were evident 2 yr after the initial pike stocking.

Horseshoe Lake (358 ha) supports a centrarchid community supplemented by walleye stocking. The northern pike population in Horseshoe Lake was augmented by stocking fingerling pike at 2.1, 1.7, and 2.0 kg/ha in 1969, 1973, and 1979, respectively (Fig. 6). Northern pike abundance indices increased by 196, 365, and 168% following the three stockings. Three years after the second stocking, pike abundance had declined to prestocking levels, but rose again following the third pike stocking in 1979. The abundance of northern pike appeared to have a negative effect on yellow perch abundance, having declined 99% by 1977, 4 yr after the second pike stocking.

Apparently, repeated failures of perch recruitment occurred. Perch abundance recovered to 20% of peak levels in 1979, but 2 yr later had again declined to 5% of peak levels. The mean weight of perch taken in sampling gill nets from Horseshoe Lake increased by 31% through 1975 and then declined to 44% of the average weight before pike were stocked. During 1968 and 1969, some perch longer than 300 mm TL were captured. Beginning in 1972, the maximum length in catches declined in each year when samples were taken until in 1981 when the largest perch captured was less than 200 mm TL.

Trends in largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*) abundance at Horseshoe Lake were similar to those of yellow perch, but varied considerably in magnitude. A decline in bass abundance was evident 3yr after the first pike stocking, and bass had declined to 90% of initial levels 5 yr after the second stocking. Declines in bluegill abundance were apparent 2 yr after the initial pike stocking, but showed evidence of recovery 3 yr after the second stocking. In 1979, 6 yr after the second pike stocking, bluegill abundance reached a peak 83% above the high levels attained before pike were stocked. Although walleye stocking continued during this period, the abundance of walleye also declined.

The repeated stocking of northern pike in a centrarchid community (Horseshoe Lake) greatly reduced the yellow perch and largemouth bass populations and to a lesser degree the bluegill population. The latter two species were quite resilient, requiring repeated stockings of their predators to suppress them; in fact, following the second stocking of northern pike, bluegills increased to levels higher than before nothern pike were stocked, even in the presence of walleye (Fig. 5).

Growth rates of walleye, largemouth bass, and bluegill were also influenced by northern pike stocking. Walleye were stocked as fall fingerlings, but second-year growth was reduced when yellow perch abundance was low. Second-year growth of largemouth bass was also reduced by perch abundance. Furthermore, first-year growth of bluegill increased 67% as perch and bluegill abundance declined and then fell to earlier levels when bluegill abundance began increasing in 1978.

Growth of younger fishes seems to be more responsive to stressors (detrimental or disorganizing stimuli; after Odum 1985) than growth of adults and may serve as a better indicator for detecting and predicting early community changes. A change in individual growth rate at a specific size is more commonly observed in the juvenile stage of fishes than among adults (Botsford 1981; Colby 1984). Only the smaller walleye showed an increased size at age following exploitation in two Ontario lakes (Deyne 1983; Reid and Momot 1985).

In Grace Lake (359 ha), which supported a percid community, the northern pike population has been augmented regularly since 1955 by stocking and by the construction of a controlled spawning area (Fig. 7). Pike abundance has increased steadily since then and by 1984 was six times greater than the mean of

TABLE 1. Interactions and observed impacts on fish communities in selected north-temperate lakes. + = an increase in abundance, or successful

Interaction and lake	Area (ha)	Mean depth (m)	MEI	Secchi transparency (m)	Species[a]									
					C	LW	RS	NP	WS	W	YP	SMB	RB	BG
Walleye–cisco														
Big Muskellunge (WI)	374	6.6	7.4	4.1	−					+				
Kentuck (WI)	403	4.1	16.3	0.6	−					+				
Tomahawk (WI)	1468	8.0	9.9	3.7	+					−				
Round (WI)	1127	7.1	10.2	5.5	−					+				
Sand (WI)	376	4.7	13.7	3.4	−					+				
Lac Court Oreilles (WI)	2040	9.1	8.4	4.6	+					−				
Grindstone (WI)	1259	6.0	14.2	3.7	+					−				
Whitefish (WI)	371	9.6	7.4	4.3	+					−				
Ten-Mile (MN)	2085	21.1	7.1	5.2						−				
Mendota (WI)	1350	6.5	31.1	2.1	+					−	+			
Menona (WI)	3938	8.3	24.4	2.1	+					−	+			
Walleye–smallmouth bass														
Lucerne (WI)	415	7.4	6.7	5.5		−	+			−		+		
Big Pine (WI)	246	3.4	11.6					+−+		+−+		−+−		
Metonga (WI)	873	8.0	11.6	7.9						−		+		
Escanaba (WI)	119	2.6	16.1	4.0				+		+		−		+
Big (MN)	704	2.7	13.8							−		−+−		
Hungry Jack (MN)	186	6.4	3.3							−	+	−+−		
Pike (MN)	328									+		−+−		
Two-Island (M)	321	3.0	12.8							−		−+−		
Lax (MN)	120	3.6	15.1	4.3				+	−	+	−	−		
Walleye–Rainbow smelt														
Lucerne (WI)	415	7.4	6.7	5.5			+			−		+		
Fence (WI)	1352	8.7	6.9	6.6			+			−				
Sucker removal														
Wilson (MN)	245	6.6	4.8	3.8					+−+	−++	−+−			
Dumbbell (MN)	177	4.1	15.9	2.1				+	−	+	−		+	
Lax (MN)	120	3.6	15.1	4.3				+	−	+	−	−		
Big Bear (MI)									+−+		−+−	0	−+−	
Northern pike manipulation														
Horseshoe (MN)	358	5.6	24.4	2.5				−+−		+	+−+			−+−
Harriet (MN)	136	8.8	20.9	2.4				−	+	+	+−			−+
Grace (MN)	359	4.3	47.0	2.0				+	−	−	−			

(i.e. stocking); − = a decrease in abundance, or unsuccessful.

Stocking		Remarks	Reference
			T. K. Kraatz, pers. comm.
		Eutrophication	R. W. Wendt, pers. comm.
	+		R. W. Wendt, pers. comm.
		Eutrophication	F. W. Pratt, Jr.. pers. comm.
		Eutrophication	F. W. Pratt, Jr., pers. comm.
−	+		F. W. Pratt, Jr., pers. comm.
−	+		F. W. Pratt, Jr., pers. comm.
−	+		F. W. Pratt, Jr., pers. comm.
−	+	Dwarf cisco present but not sampled	
			C. L. Brynildson, pers. comm.
			C. L. Brynildson, pers. comm.
	+		H. W. Carlson, pers. comm.
			Inskip and Magnuson 1983
	+	Crayfish increased	H. W. Carlson, pers. comm.
		Walleye and northern pike introduced	Kempinger et al. 1975
	+	Walleye and northern pike stocked, suckers removed	
	+		R. W. Wendt, pers. comm.
			H. W. Carlson, pers. comm.
		Walleye and perch size increased as suckers recovered	Johnson 1977
	+	Walleye and muskellunge stocked confounding analysis	
	+	Walleye and northern pike stocked	
		90% of adult white suckers removed in 1943 and again in 1955–57; yellow perch and rock bass benefited from removal; smallmouth bass did not	Schneider and Crowe 1980
	+	Growth rates of all species influenced after pike introduction	
	+	Pike removed, muskellunge stocked macrophytes recovering	
	+?	Northern pike stocked, perch size has declined	

TABLE 1. (*concluded*)

Interaction and lake	Area (ha)	Mean depth (m)	MEI	Secchi transparency (m)	Species[a]									
					C	LW	RS	NP	WS	W	YP	SMB	RB	BG
Eutrophication														
Osakis (MN)	2537	7.4	27.3	1.7				+-		−	−			+
Gull (MN)	3811	8.1	18.4	2.4				+		−	+			
Sallie (MN)	490	5.6	47–60	4.2–1.8-3	−				−	−	−	−		+?
Smelt–whitefish														
Twelvemile (Ont.)	463	10.6	3.21	5.2		−	+							
Elliot (Ont.)	606	13.8	5.0	5.1		−	+							

[a]C = cisco; LW = lake whitefish; RS = rainbow smelt; NP = northern pike; WS = white sucker; W = walleye; YP = yellow perch; SMB = fry; WFG = walleye fingerling.

three surveys from 1950 to 1945. The response of the fish community to the augmented pike population was quite drastic until 1964 when the fish community seemed to stabilize. Both yellow perch and white sucker declined to a new low as northern pike increased.

The phase diagrams for Grace Lake (Fig. 8) provide insight into the relationships between the four fish species, but must be interpreted with caution. While we have plotted all possible relationships, some may be artifactual. We have reasonable expectations that northern pike predation controls the abundance of yellow perch and white sucker. If we assume that the fish community composition was relatively stable prior to the pike introduction, we have a strong indication of a movement to a new set of "attractor domains" or stable nodes (Holling 1973) for predator–prey relationships following the introduction.

The abundance of walleye increased following the pike introduction before decreasing and stabilizing. We expect that the relationship of walleye and pike is mediated by the changes in the forage base induced by the changing abundance of northern pike.

The sport fishing yield of walleye from Grace Lake increased 2.5 times from 1958 through 1960 (Fig. 7), and catch per man-hour increased 67% probably as a result of a reduction in suitably sized walleye prey (Wesloh and Olson 1962), making walleye more vulnerable to angling (Forney 1980). However, a decline in walleye abundance (66%) was evident 3 yr after the second pike stocking in 1973. Walleye abundance had not recovered by 1983. The abundance of yellow perch declined 85% (Table 1) and the mean size of yellow perch captured by experimental gill nets declined steadily from 0.15 kg in 1948 to 0.06 kg in 1984, a decline of 60%.

Abundance of white suckers, walleye, and yellow perch declined noticeably with the buildup of northern pike. White suckers declined by 72% and yellow perch by 85% from levels observed before northern pike became established. The abundance of walleye declined by 80% from peak levels, but apparently recovered in recent years probably as a result of intensive stocking (Fig. 7).

The repeated stocking of northern pike in Grace Lake, a percid community, reduced yellow perch significantly as they did in a centrarchid community (Horseshoe Lake). Northern pike also suppressed white sucker, but like yellow perch, they declined gradually (about 10 yr). However, sport fishing for walleye improved as yellow perch declined, likely making walleye more vulnerable to angling as a major food source declined.

Disturbances due to species removals

Walleye removals

Beginning in 1980, the walleye populations were perturbed by different harvest strategies in two experimental lakes in north-central Ontario. In Henderson Lake (151 ha), the walleye stock collapsed due to pulse fishing in which a total of 15 kg/ha (89%) of the walleye biomass was removed over a 3 yr period. During and since the removal (a total of 6 yr), abundance of northern pike and white suckers based on mark and recapture population estimates has not increased, nor have these species replaced the walleye biomass lost from the system (Reid 1985; OMNR 1985, 1986). Also, there was no apparent increase in growth of white suckers following walleye removal in Henderson Lake (McIver 1985).

In Savanne Lake, walleye were harvested by incrementally increasing fishing pressure on selected intermediate-sized fishes. During the first increment of fishing pressure (1980–85) annual harvests equal to estimates of walleye annual adult production (about 1.8 $kg \cdot ha^{-1} \cdot yr^{-1}$) had no obvious influence on the numbers of northern pike or white suckers. In both Henderson and Savanne lakes, northern pike and white suckers were not harvested except for mortalities caused by the experimental treatments. In Savanne Lake, walleye catches in

Stocking			
WFY	WFG	Remarks	Reference
		Walleye spawning failed (periphyton) Agricultural runoff and shoreline development	Loftus and Hulsman 1986
	+	Walleye spawning failed (periphyton) Agricultural runoff and shoreline development	Loftus and Hulsman 1986
	+?	Walleye spawning failed; municipal sewage disposal until 1972; bullheads abundant until sewage was diverted	OMNR 1984

smallmouth bass; RB = rock bass; BG = bluegill; WFY = walleye

trapnets did not decrease despite about a 27% reduction (according to population estimates) in vulnerable size walleye. Preliminary evidence does suggest that the abundance of YOY yellow perch has increased.

It may be premature to conclude that the sucker populations will not increase in Henderson and Savanne lakes. White suckers mature at age 5 in Wilson Lake, but it took 7 yr before the biomass of adult suckers showed a major increase after the large scale removal (Johnson 1977). In addition, growth rates showed little change in Wilson Lake with the exception of one year class.

The shorter generation time of northern pike leads us to expect to see a more rapid response in population size. The lack of response to date suggests that competition with walleye is not important in the regulation of pike population size in these lakes. This hypothesis is further supported in Escanaba Lake, Wisconsin, where both walleye and northern pike were harvested by anglers. Since there was no significant relationship (r = 0.166) between the mark–recapture estimated densities of adult walleye and adult northern pike during 1959–69, separate factors may be controlling their abundance. During this period there was a fourfold variation in walleye density and a sevenfold variation in northern pike abundance. In recent years (1981–84), average adult walleye densities were more similar to those found during the 1959–69 period, while northern pike abundance was lower than in many of the years from 1959 to 1969.

Northern pike removals

In Heming Lake, Manitoba, an intense northern pike fishery was initiated in 1945 to disrupt the life cycle of *Triaenophorus crassus*, a parasite of both coregonids and northern pike. Lawler (1960 and pers. comm.) reported that after a few years of removing 2.2 kg/ha of northern pike during spawning runs with hoop nets, they were as abundant as ever. In the 1950's, the annual pike harvest was maintained at close to 3.4 kg/ha (but reached 4.5 kg in 1958) using gill nets and continually reducing the mesh size. Northern pike could not be exterminated, even by fishing in one year the equivalent of one set of 219 817 metres of gill nets in this 259-ha lake. Northern pike were removed by hoop nets, gill nets, trammel nets, and rotenone without killing whitefish, except for sampling their cyst content (G. H. Lawler, pers. comm.). After about 14 yr (ca. 1959), whitefish were free of *Triaenophorus* because northern pike were too small to feed on a sufficient number of infected whitefish to complete the parasite's life cycle (K. H. Doan, interdepartmental memorandum (1978)). Before intensive fishing began (1945 and a few years after), there were many large pike over 9 kg in the catches, and northern pike started to spawn at about 41 cm and at ages 3 and 4. Intense fishing and reduction in mesh size reduced the average size of pike in the catch to about 26.3 cm and less than 227 g. Also, their growth rate increased, and in September of their first year of life, male pike matured, indicating that they would spawn the following spring at age 1. Intensive fishing practically reduced the northern pike population to the YOY year class (G. H. Lawler, pers. comm.).

When northern pike control began at Heming Lake, white suckers were also removed at "normal" sizes and at about 2.2 kg/ha (K. H. Doan, interdepartmental memorandum (1978)). In the last year of intense pike removal, sucker harvests increased to about 11 kg/ha and individual fish averaged about 15.2 cm TL. Yellow perch increased similarly in abundance and size. The very abundant suckers, yellow perch, and trout-perch (*Percopsis omiscomaycus*) contributed to the fast growth of pike. Conversely, very small pike did not eat cisco or whitefish in the quantities consumed by medium and large pike, consequently disrupting the *Trianophorus* life cycle. The Heming Lake case history illustrates that when habitat is optimum for reproduction, intensive removal may not eliminate the species but only initiate a compensatory response resulting in a faster turnover of the population.

TABLE 2. Species interactions due to human disturbances, primarily species add

Manipulation	Lake	Response
Species additions		
Rainbow smelt introduced	Michigan	Cisco declined
		Bloater *C. hoyi* eaten by rainbow smelt
Rainbow smelt introduced	Huron	Cisco declined
Rainbow smelt introduced	Superior	Cisco declined; cisco eate rainbow smelt
European smelt introduced or present	Chudskoye; Syamozero; Pskovshoye (USSR)	European smelt and cisco abundance inversely affected
Rainbow smelt introduced	Twelvemile (Ont.)	Whitefish declined; coregonids eaten by rainbow smelt
Rainbow smelt introduced	Elliot	Coregonids eaten by rainb smelt; whitefish yield a recruitment inversely related to smelt abunda
Rainbow smelt introduced	Simcoe	Whitefish recruitment an yield inversely related smelt
Rainbow smelt introduced	Fish River lakes (ME)	Whitefish populations declined in 7 out of 7 l where smelt were introduced
Rainbow smelt	Lucerne (WI)	Whitefish population collapsed; drastic decli walleye reproduction a recruitment
Rainbow smelt introduced	Fence	Drastic decline in walley reproduction and recruitment
Rainbow smelt introduced	Champlain (114 046 ha)	No negative effect on wa

ecies additions and removals, and habitat perturbations.

se	Reference(s)	General comments
	Smith 1972	Cisco and rainbow smelt abundance inversely related
aten by	Stedman and Argyle 1985	Smelt predation on bloater has potential to negatively influence bloater population in L. Michigan
	Smith 1972	Cisco and rainbow smelt abundance inversely related
isco eaten by	Smith 1972; Anderson and Smith 1971; Ryder and Edwards 1985; Selgeby et al. 1978; Swenson 1978	Cisco and rainbow smelt abundance inversely related
nd cisco ersely	Reshetnikov 1979	
ed; en by	Loftus and Hulsman 1986; K. Armstrong, pers. comm.	Whitefish population experiencing recruitment failure
by rainbow h yield and versely t abundance	Loftus and Hulsman 1986; K. Armstrong pers. comm.	
ment and related to	Loftus and Hulsman 1986; D. O. Evans, unpubl. manuscr.	
tions ut of 7 lakes ere	Warner and Fenderson 1963	
tion tic decline in luction and	This study (Table 1)	Walleye fingerling successfully in L. Lucerne; walleye replaced by smallmouth bass in recent years
n walleye nd	This study (Table 1)	
ct on walleye	A. Schiavone Jr., NY DEC, pers. comm.	Spatial segregation may reduce the intensity of interactions (adult smelt from larval walleye)

TABLE 2. (*continued*)

Manipulation	Lake	Resp
Northern pike introduced	Horseshoe (MN) (centrarchid community)	Yellow perch bass, and b yellow perc by 99%
Northern pike introduced	Grace (MN) (percid community)	Yellow perch sucker decl
Walleye introduced	Boyd Reservoir (CO)	Walleye incre crappie dec
Walleye introduced successfully as eyed-eggs in a centrarchid community	Scugog, Rice	Good walleye fishery esta
Species removals		
Walleye (only) removed ($1.8\ kg \cdot ha^{-1} \cdot yr^{-1}$ removed for 6 yr)	Savanne (Ont.) (364 ha)	No major cha pike or wh abundance and recaptu estimates)
Walleye population collapsed ($15\ kg \cdot ha^{-1} \cdot yr^{-1}$ or 89% of biomass removed in 3 yr) due to pulse fishing	Henderson (Ont.) (151 ha)	No major cha pike or wh abundance and recaptu
Both walleye and northern pike harvested by anglers	Escanaba (WI)	No relationsh walleye an abundance recapture p estimates)
Northern pike removed	Heming (MAN)	Northern pik eliminated and large a in good nu habitat; wh yellow per abundance

Response	Reference(s)	General comments
ow perch, largemouth ss, and bluegill declined; llow perch declined 99%	Anderson and Schupp 1986 (table 1)	Early growth rate changes of walleye, largemouth bass, and bluegills were observed; largemouth bass and walleye growth declined, bluegill growth increased as yellow perch and bluegill abundance declined; northern pike supplemented by stocking
ow perch and white cker declined	Wesloh and Olson 1962 (table 1)	Yellow perch and white sucker response was slow (10 yr for changes to occur); northern pike has been augmented regularly since 1955 by stocking and by the construction of a controlled spawning area
eye increased; black ppie declined	Puttmann and Weber 1980	Habitat favoured walleye, erratic water level fluctuations, turbidity, lack of rooted aquatic vegetation, and shallow sand and mud shorelines
l walleye recreational hery established	C. Lewis, pers. comm.	No black crappie in these lakes; both lakes are large (7000–10 000 ha); thus, spatial segregation may have prevented intense negative interactions between the walleye and centrarchids
ajor change in northern ke or white sucker undance after 6 yr (mark d recapture population timates)	OMNR 1986	YOY walleye perch abundance has increased
ajor change in northern ke or white sucker undance after 6 yr (mark d recapture estimates)	Reid 1985; Reid and Momot 1985; OMNR 1985; McIver 1985	Ninespine stickleback (*Pungitius pungitius*) population collapsed only in exploitation phase
elationship between lleye and northern pike undance (mark and capture population timates)	This study (Table 1)	Between 1959 and 1969 there was a fourfold variation in walleye density and a sevenfold variation in northern pike abundance
hern pike could not be minated with fishing gear d large amount of effort good northern pike bitat; white sucker and llow perch increased in undance	Lawler 1960 and pers. comm; K. H. Doan, pers. comm.	After about 14 yr, *Trianophorus crassus* life cycle broken because northern pike were too small to feed on significant number of whitefish

TABLE 2. (*Continued*)

Manipulation	Lake	Response
Northern pike and macrophytes removed followed by introduction of walleye and muskellunge	Harriet (MN) (typical centrarchid lake)	Yellow perch and whit sucker abundance inc dramatically; walley successfully introduc with muskellunge, resulting in a decrea yellow perch, white s (by 80%), and an in in bluegills
White sucker removed (85% reduction in biomass or 34 kg/ha), primarily adults	Wilson (MN)	Abundance of yellow p and walleye increase effect of white sucke removal evident 18 y yellow perch standin removed 15-fold, an walleye standing cro increased by one thi
White sucker removed (53.0 kg/ha)	Lax (MN)	Yellow perch declined due to predation by northern pike and st walleye; walleye an northern pike increa
White sucker population reduced 92% from harvests of 8.7 kg/ha (1970) and 11.7 kg/ha (1977–78); walleye successfully introduced 1 yr after second white sucker removal; walleye became very abundant	Dumbbell (MN)	Yellow perch declined 85%; rock bass incr 12-fold
White suckers removed; about 90% of the adults were removed with trap nets in 1943 and again in 1955–57; white sucker recovery took 8 and 3 yr, respectively	Big Bear (MI)	Yellow perch and rock increased followed l successful walleye introduction; largem and smallmouth bas not benefit from white sucker remov

ponse	Reference(s)	General comments
and white dance increased ; walleye were introduced llunge, a decrease of n, white suckers nd an increase	This study (Table 1)	Sodium arsenite was frequently applied as an aquatic herbicide to maintain swimming beaches; macrophytes were nearly eliminated; four successive stockings of walleye fingerlings were successful and a dense population of fast-growing walleye developed; walleye reached total lengths by age 4 that are usually reached at age 7 in Minnesota's prime walleye waters
yellow perch increased; ite sucker, dent 18 yr later; h standing crop -fold, and ding crop one third	Johnson 1977; This study (Table 1)	Rock bass not present; major changes in feeding habits of fishes of various ages documented; white sucker biomass (mainly adults) recovered to within 80% of preremoval levels, 18 yr earlier; growth rates of percids increased and then decreased as they became more abundant
declined 27% tion by e and stocked lleye and e increased	This study (Table 1)	10 yr after removal, white sucker abundance was about 20% of the preremoval levels; walleye abundance six times greater than before white sucker removal; northern pike abundance increased by 28-fold over preremoval level
declined by ass increased	This study (Table 1)	
and rock bass llowed by valleye ; largemouth outh bass did from r removal	Schneider and Crowe 1980; J. Schneider, pers. comm.	MDNR rule of thumb: at least 80% of white sucker population must be removed to be effective

TABLE 2. (*concluded*)

Manipulation	Lake	Response
Brown bullhead removed (135 kg)	Cole (Ont.) (32 ha)	Sevenfold increase in largemouth bass (age and older, predomina the 1975 year class)
Hatitat perturbations		
Eutrophication, sedimentation, and macrophyte buildup	Indian River system (NY)	Black crappie increased walleye declined
Eutrophication, sedimentation, and macrophyte buildup	Georgian Bay Port Severn area (Ont.)	Black crappie increased walleye declined
Sewage effluent entered lake following primary and secondary treatment	Sallie (MN)	Fish community change from percid to centra to ictalurid and then reversed following w treatment (phosphoru removal using lime)
Water level drawdown	Shebandowan (Ont.)	Cisco growth rate relati high (Fig. 1), walley at age declined over 13 yr

onse	Reference(s)	General comments
ase in ass (age 2+ edominately class)	OMNR 1982	Population increase was due almost exclusively to the success of the 1975 year class of bass which made up 85% of the population; the success of the 1975 year class was not as spectacular in five other lakes in which bullheads were not removed, suggesting that a factor other than weather was responsible for the large 1975 year class in Cole L.
ncreased; ned	Schiavone 1981, 1983; Mills and Schiavone 1982	
ncreased; ned	Hogg 1975, 1976; LaFrance 1980	
y changed o centrarchid nd then owing water osphorus g lime)	This study (Table 1); Olson and Koopman 1976	Macrophytes were removed using mechanical harvesters, and algal control was attempted using copper sulfate; estimated a standing crop of bullheads as high as 1146 kg/ha of which 96% were black bullheads
te relatively , walleye size ed over past	Wepruk 1983; L. Godwin, pers. comm.	Whitefish population reduced to very low abundance due to overfishing; immature whitefish growing more rapidly now than in the past

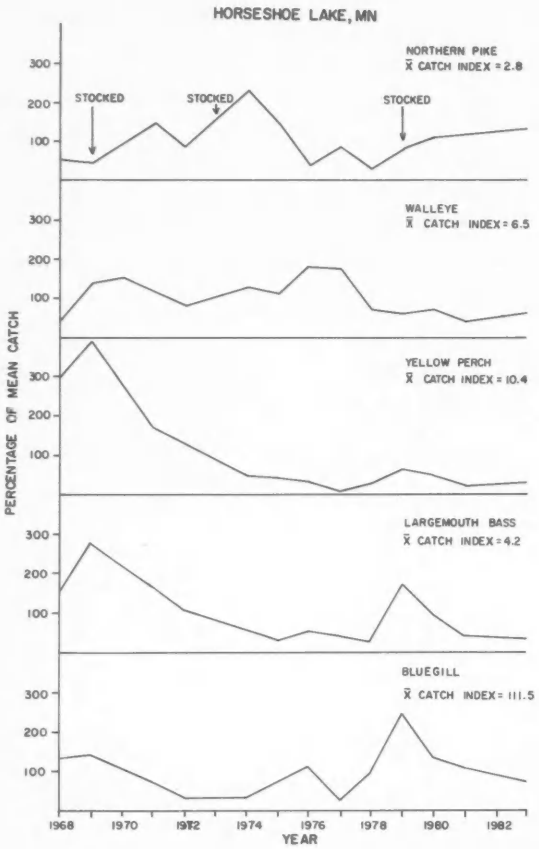

FIG. 6. Changes in compostion of survey net catches (number/lift) following the stocking of northern pike into Horseshoe Lake, Minnesota. Mean ($\bar{x}$) catch index is the mean catch for each species for all surveys.

Harriet Lake (136 ha) in urban Minneapolis, Minnesota, provides another example of community changes following northern pike removal (Fig. 9). The lake is a typical centrarchid lake located in city parklands, and roadways surround the entire shoreline. A survey in 1948 indicated high abundance of northern pike maintained by stocking. Yellow perch and bluegills were abundant. White suckers were present in low numbers, but there were no walleye, although records indicate that they had been stocked.

During the 1950's and early 1960's, sodium arsenite was frequently applied as an aquatic herbicide to maintain swimming beaches. Macrophytes were nearly eliminated, and residual arsenic compounds apparently suppressed plant regeneration through the early 1980's. The northern pike population declined and yellow perch increased (Fig. 9). Beginning in 1961, a controlled spawning area was created and operated for northern pike. The pike population increased, reaching peak numbers in 1974. Yellow perch abundance declined to very low levels and sucker abundance increased slightly.

A decision was made to manage the lake for muskellunge (*Esox masquinongy*) and operation of the northern pike spawning area was discontinued after 1974. Northern pike were

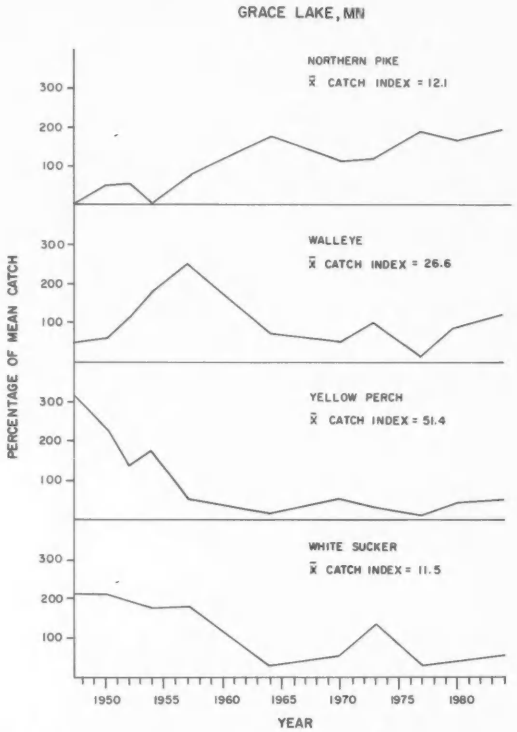

FIG. 7. Changes in composition of survey net catches (kg/lift) following introduction of northern pike into Grace Lake, Minnesota. Mean ($\bar{x}$) catch index is the mean catch for each species for all surveys.

removed by trapnet from 1975 through 1979. The removal of 1398 fish (13.9 kg/ha) apparently eliminated pike from the lake. From 1979 through 1983, an average of 0.5 muskellunge fingerlings/ha was stocked annually.

Following removal of pike in 1979, abundances of yellow perch and white sucker were at the highest levels ever observed (Fig. 9). Four successive stockings of fingerling walleye (1974–77) were successful, and a dense population of fast-growing walleye developed. Walleye reached total lengths by age 4 that are usually reached at age 7 in Minnesota's prime walleye waters. Bluegill abundance declined to very low levels (nine fish captured in 1979).

During the most recent survey (1984), walleye abundance was still high, but only 10 yellow perch were captured and white sucker abundance had declined by 80%. In contrast, the bluegill population had expanded, exceeding the previous high catch by 48% (Fig. 9). It will be interesting if over the next several years, the combination of walleye and muskellunge is able to prevent the white sucker population in Harriet Lake from expanding.

Removal of northern pike from both Heming and Harriet lakes resulted in an increased abundance of yellow perch and white suckers (Table 2). When walleye and muskellunge replaced northern pike as predators, yellow perch and white sucker again decreased, and bluegills increased. The removal of aquatic macrophytes likely accounted in part for the excellent growth of walleye (Table 2).

White sucker removals

Sucker removal from three Precambrian shield lakes in

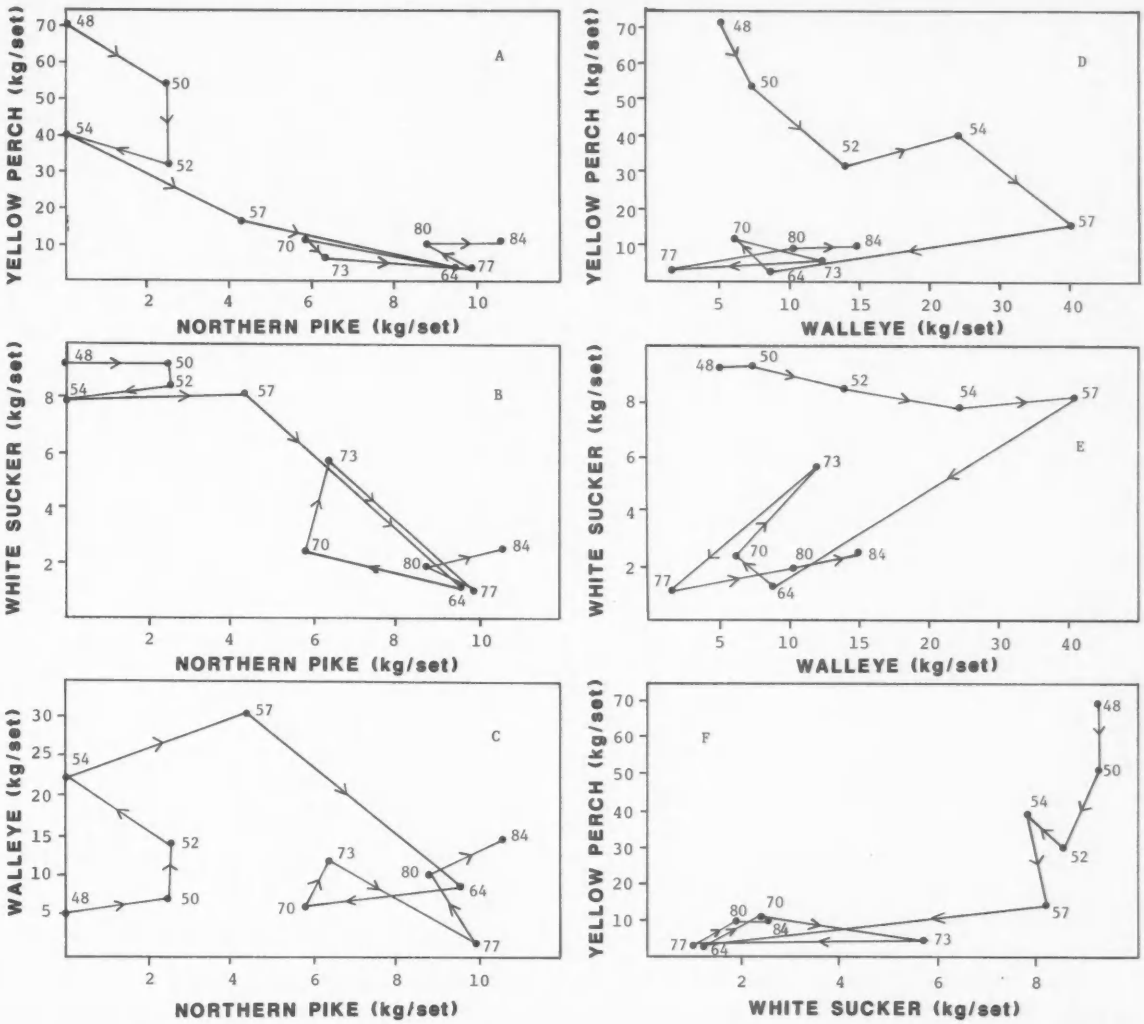

FIG. 8. Phase diagrams of species abundances over time in Grace Lake, determined by catches in standard gillnet sampling. The numbers within the figures illustrate years of sampling.

northern Minnesota yielded dissimilar but positive results. In only one of these lakes (Wilson Lake, 245 ha) were the changes attributed to sucker removal (Johnson 1977) evident 18 yr later (Fig. 10). Removal of 85% of the sucker biomass (34 kg/ha), primarily adults in Wilson Lake, was followed 7 yr later by a 15-fold increase in the standing crop of yellow perch and a one-third increase in the standing crop of walleye.

The phase diagrams of species abundance in Wilson Lake (Fig. 11) show a relatively stable relationship between species prior to sucker removal in the spring of 1966. In later years there is some indication that the populations of white suckers and yellow perch are again stabilizing in relation to each other. The relationship of walleye to the other species does not show any tendency to stabilize; however, the dynamics of walleye abundance may well be driven primarily by angling and the variable year class strengths as described by Johnson (1977).

Prior to sucker removal, little recruitment of suckers to the adult population was evident, but several years after removal the sucker population was dominated by newly recruited adults. Surveys 11 and 18 yr after sucker removal indicate a population once again dominated by adults with a biomass about 80% of the preremoval level (Fig. 10).

The growth rates of walleye and yellow perch in Wilson Lake increased for 5 yr after sucker removal, reflecting the increased availability of forage, but declined thereafter as percid abundance increased. Benthos abundance did not change, but in the second year after sucker removal the abundance of young perch was greater than during baseline years and generally remained above baseline levels for the next 5 yr. The abundance of small fish (suckers, minnows, and darters) captured in shoreline seining was lower after sucker removal.

The longer term increase in all three species since sucker removal raises the question as to whether the carrying capacity of the lake for these species increased. The stickleback

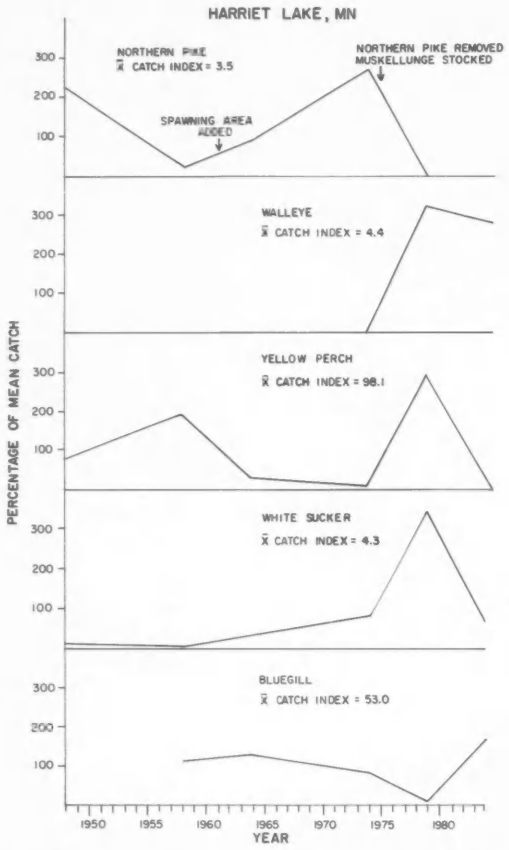

FIG. 9. Changes in composition of survey net catches (number/lift) following the development of northern pike spawning area and later the removal of northern pike from Harriet Lake, Minnesota. Mean ($\bar{x}$) catch index is the mean catch for each species for all surveys.

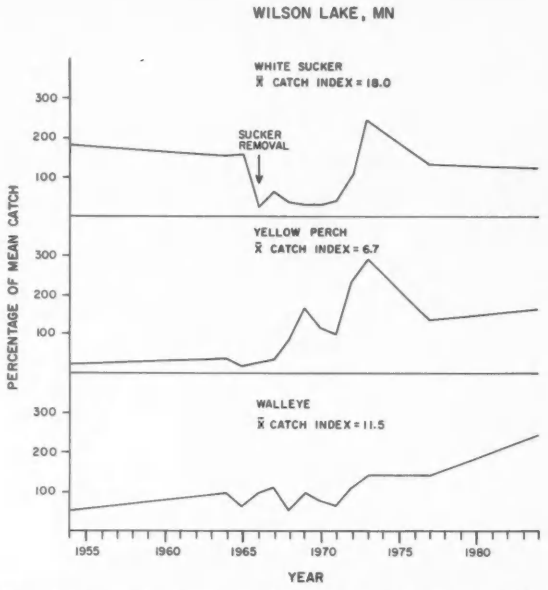

FIG. 10. Changes in compostion of survey net catches (number/lift) following removal of white suckers from Wilson Lake, Minnesota. Mean ($\bar{x}$) catch index is the mean catch for each species for all surveys.

population virtually disappeared in Henderson Lake in the early years of the walleye removal study (Reid and Momot 1985). Since only the perch abundance changed in the early part of the Henderson study, the decline of stickleback is attributed to interactions with the perch populations. In Wilson Lake, however, the importance and composition of the fish part of the walleye ration changed. Larger walleye (>229 mm) increased their consumption of YOY perch and decreased their consumption of minnows and darters. Smaller walleye increased their consumption of minnows and darters. YOY perch were not important in either period for YOY walleye. The increased perch population was supported by increased use of mayflies and zooplankton.

It appears that most diet changes reduced inter- and intraspecific competition and involved replacement of smaller food items with larger ones, increasing the bioenergetic efficiency of foraging. The lower abundance of small fish (minnows, darters, and suckers) is attributed to increased predation and possibly to competition with young perch. In effect, the food web would seem to be more efficient in directing energy flow to support of percids.

The structure of the preremoval food web suggests that the recovering sucker population should preempt benthic food resources and cause reductions in the perch and walleye populations through competition. The maintenance of the increased perch population and the dependent walleye population therefore requires additional explanation after the sucker population's recovery. As the perch population built up, population fecundity presumably increased. Population growth was proportional to apparent year class strength (seine index) from 1966 to 1968. The recruitment return from year class strength changed after this point, and the largest year classes produced the lowest returns (large perch/YOY index, 1969–73). We suggest that the perch population came to a temporary equilibrium with new level of benthic and planktonic food resources during the time period 1968–71, based on the pattern in the phase diagrams (Fig. 11). After that point, however, the increase in suckers should have caused a reduction in perch abundance. The abundance of perch YOY in 1971 was based on a low abundance of large perch and resulted in an approximate tripling of the abundance of large perch. Subsequent YOY indices of abundance are much lower than expected considering the population fecundity. We suggest that cannibalism is the only explanation for the low abundance of YOY and the continued maintenance of a large perch stock after 1971.

Successful sucker removal in the two other Minnesota lakes did not result in the desired increase in abundance of yellow perch. In Lax Lake (120 ha), the abundance of suckers 10 yr after a removal of 53.0 kg/ha in 1969–70 was about 20% of preremoval levels. The abundance of yellow perch had also declined to 27% of preremoval levels. Predation by stocked walleye and northern pike may have prevented the yellow perch from increasing. Walleye were introduced into Lax Lake in 1955 and have been stocked regularly since. The most recent survey indicated that walleye abundance was six times that at the time of the last survey before sucker removal. Northern pike

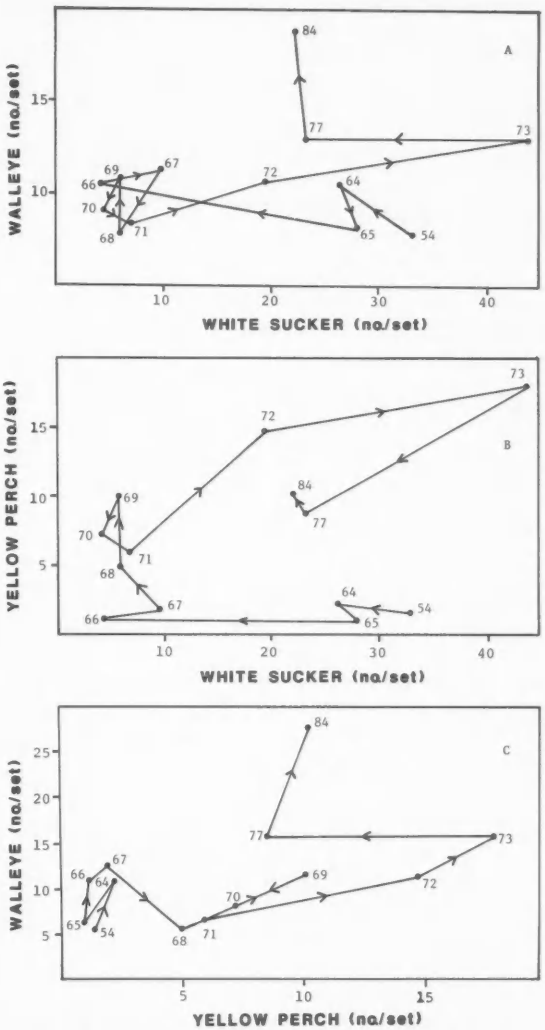

FIG. 11. Phase diagrams of species abundances over time in Wilson Lake, determined by catches in standard gillnet sampling. The numbers within the figures illustrate years of sampling.

were stocked regularly from 1963 through 1968. Northern pike abundance in the most recent survey was 28 times that of the preremoval survey.

In the second case (Dumbbell Lake, 177 ha), suckers were removed in 1970 (8.7 kg/ha) and in 1977–78 (11.7 kg/ha). A survey in 1983 indicated a reduction in sucker abundance to 92% of preremoval levels. In contrast with the results at Wilson Lake, the abundance of yellow perch declined by 85%, while the abundance of rock bass (*Ambloplites rupestris*) increased by a factor of 12. Walleye were successfully introduced 1 yr after the second sucker removal, and the 1983 survey indicated an exceptionally high walleye population. Predation by the large walleye population may have prevented perch from responding to sucker removal, thus allowing the rock bass population to expand. White sucker removal (90%) from Big Bear Lake, Michigan, resulted in increased abundances of both yellow perch and rock bass in the absence of walleye (Schneider and Crowe 1980). The increase in forage fish may have permitted the successful introduction of walleye now present in Big Bear Lake (J. Schneider, Michigan Department of Natural Resources (MDNR), pers. comm.).

These case histories suggest that the removal of undesirable fish species may reduce competition for a desired target species which may increase in abundance if habitat conditions are right and a sufficient number of competitors are removed. The MDNR rule of thumb for white sucker removal is that at least 80% must be removed to be effective (J. Schneider, MDNR, pers. comm.). The Wilson, Dumbbell, and Big Bear Lake case histories support this rule. In all three lakes there was a significant increase in the abundance of more highly preferred species, or stocking predators was successful following a major removal (>80%) of white suckers.

Brown bullhead removals

Positive results from a brown bullhead (*Ictalurus nebulosus*) removal project were achieved at Cole Lake (32 ha), Ontario (OMNR 1982). In 1974, 1060 (135 kg) bullheads were removed from Cole Lake to reduce competition with, and possible predation on, largemouth bass. Assessment work conducted during 1978 indicated a sevenfold increase in the number of adult largemouth bass (ages 2+ and older from 1974 to 1978). The population increase was due almost exclusively to the success of the 1975 year class of bass which made up 85% of the population. In five other lakes studied during the summer of 1978 in which bullheads were not removed, the success of the 1975 year class was not as spectacular. This suggests that weather was not solely responsible for the success of largemouth bass in Cole Lake in 1975, but rather that their success was due to the removal of bullheads in 1974.

Habitat Perturbations by Humans

Eutrophication, erosion, chemicals, water level fluctuations, and their subsequent influences on macrophyte abundance, turbidity, food availability and spawning, and nursery areas can significantly favour the dominance of one species over another.

R. F. Carline (unpubl. data) conducted an analysis of 88 lakes in 12 northwest Wisconsin counties to investigate the association of various species with each other and with physical–chemical data. The only physical index that was positively related to walleye biomass was percent of lake bottom which was rubble; otherwise, walleye biomass was negatively related to aquatic macrophytes and other abiotic productivity parameters (conductivity, alkalinity, and pH), which were positively related to macrophyte abundance.

Carline also found that the relative biomasses of rock bass and smallmouth bass, like walleye, were negatively correlated with macrophytes whereas relative biomasses of esocids, largemouth bass, and bluegills were positively correlated with this factor.

Eutrophication

In waters undergoing accelerated eutrophication and buildup of macrophytes, there is some evidence that black crappie (*Pomoxis nigromaculatus*) may have a negative influence on walleye recruitment (Schiavone 1981, 1983; Mills and Schiavone 1982). The recruitment failures these authors observed in Black Lake and the Indian River system in Upper New York may also have occurred in the Port Severn area of Georgian Bay, Lake Huron (Hogg 1975, 1976; LaFrance 1980).

A negative correlation between abundances of black crappie

and walleye was also observed in a series of 383 lake surveys from central Minnesota. The inverse relationship was strongest in lakes with mean depth exceeding 3.3 m. Water clarity was positively correlated with mean depth, and the density of macrophytes is usually greater in clear waters, suggesting that both water clarity and subsequent buildup of macrophytes favoured black crappie over walleye.

In Little Arbor Vitae Lake, Wisconsin, Kempinger (1972) reported a negative association between black crappie abundance and walleye year class strength from 1965 to 1969. During those years, crappies of the 1964 year class dominated the electrofishing catches, and no walleye year classes were established. Conversely, walleye replaced black crappie after walleye were introduced into Boyd Reservoir, Colorado (Puttmann and Weber 1980). Boyd Reservoir is characterized by erratic water level fluctuation, turbidity, lack of rooted aquatic vegetation, and shallow sand or mud shorelines.

Usually when vegetation dominates the littoral zone, centrarchids are dominant over percids. Walleye were introduced successfully as eyed-eggs, however, into two centrarchid communities (Lake Scugog, 7030 ha, and Rice Lake, 10 010 ha) void of black crappie in eastern Ontario (C. Lewis, OMNR, pers. comm.). This leads to further suspicion that black crappie have a negative influence on walleye recruitment. The two centrarchid lakes in which the walleye were successfully introduced were also large (7000-10 000 ha); thus, spatial segregation may have prevented intense interactions between the walleye and centrarchids.

Fish communities may undergo extensive changes in species composition when subjected to sewage effluent, but reduction in sewage effluent may result in restructuring the community towards its original composition. For example, Sallie Lake (490 ha) in northwestern Minnesota received sewage effluent subjected to primary and secondary treatment from a town with a population of about 6000 through 1972. Summer residents may have tripled the load of effluents. After 1950, the effluent was treated with lime to remove phosphorus. Macrophytes were removed from the lake by mechanical harvesters and algal control was attempted with copper sulfate. Recovery of the system was evident within 3 yr of completion of the sewage diversion in 1973. Total alkalinity in 1949 was 202 mg/L, rose to 262 mg/L by 1968, and by 1975 was down to 179 mg/L. Water clarity went through similar changes. A Secchi disk was visible at 4.2 m in 1949, 1.8 m in 1968, and 3.2 m in 1975.

Based on size and morphometry of the basin, Sallie Lake should contain a fish community dominated by percids. The earliest survey (1949) indicated high populations of walleye, yellow perch, and white sucker (Fig. 12). Northern pike were a common predator and centrarchids were well represented, with bluegill, black crappie, and largemouth bass being common. Cisco and smallmouth bass were reported present. After treatment began, walleye, perch, and sucker abundance indices declined and by 1975 were 14, 34, and 20%, respectively, of peak abundance (Fig. 12). Cisco and smallmouth bass were last reported in 1954. Bluegill abundance rose through 1968 but declined to its lowest level in 1975. All three species of bullheads were present in low numbers during early surveys but by 1968 had expanded to extremely high abundance. Olson and Koopman (1976) estimated a standing crop of bullheads as high as 1146 kg/ha, of which 96% were black bullheads (*Ictalurus melas*), repeating the eutrophication-induced succession scenario described by Colby et al. (1972).

By 1981, walleye, perch, sucker, and bluegill populations

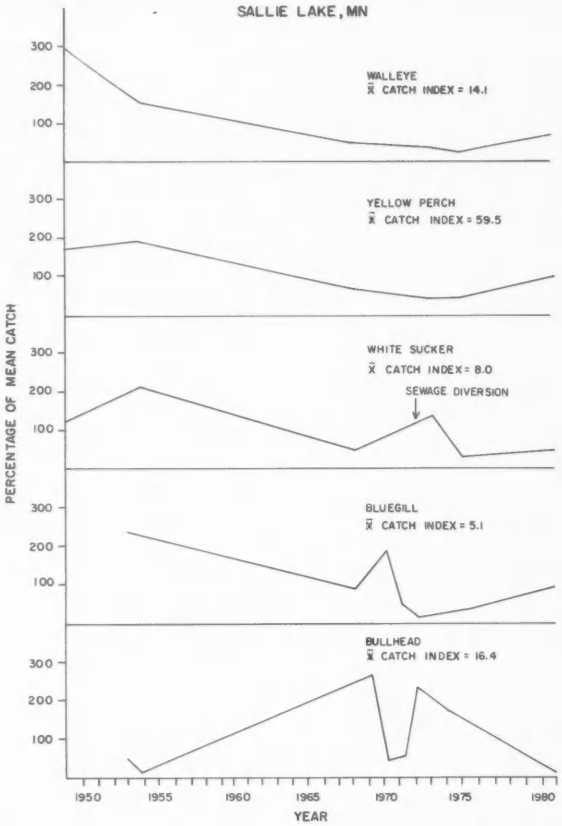

FIG. 12. Changes in composition of survey net catches (number/lift) resulting from accelerated eutrophication and following sewage diversion in Sallie Lake, Minnesota. Mean ($\bar{x}$) catch index is the mean catch for each species for all surveys.

showed evidence of recovery from the 1975 lows. Walleye abundance had tripled, perch nearly doubled, suckers had increased by 68%, and bluegills were 2.8 times as abundant as the 1975 lows. By 1975, bullhead abundance had declined drastically and by 1981 was at the low levels observed through the mid-1950's. In contrast with dominance by black bullheads in 1971, yellow bullheads (*Ictalurus natalis*), a species favouring water clarity (Scott and Crossman 1973), made up 53% of bullheads in the survey.

A comparison of population changes associated with habitat degradation which have occurred over the last half century in the Great Lakes with those of smaller inland lakes suggests some similarities. The recovery of walleye in Sallie Lake following sewage diversion (this paper) parallels the Bay of Quinte walleye recovery following reduced phosphorus loading (Minns et al. 1987). Weather (cold winter) was also a factor in the Bay of Quinte recovery; the cold winter of 1977–78 apparently collapsed the local white perch (*Morone americana*) stock to the advantage of the walleye (Hurley 1986; Minns et al. 1987). Also, increased eutrophication, sedimentation, and subsequent buildup of macrophytes appeared to favour black crappie over walleye in the Indian River System of New York (Mills and Schiavone 1982; Schiavone 1981, 1983). Similarly, these types

of changes are occurring in the Port Severn area of Georgian Bay (Olver et al. 1982).

Changes in turbidity can have a selective influence on species composition. Species such as walleye, sauger (*Stizostedion canadense*), trout-perch, white crappie (*Promoxis annularis*), goldeye (*Hiodon alosoides*), and most ictalurids occupy turbid environments. Walleye appear to have a negative impact on centrarchids in Wisconsin lakes having dark-stained water and a low density of macrophytes (R. F. Carline, unpubl. data).

The size of a lake may influence the intensity of interactions and determine species dominance. Percid community structures have persisted in nine Minnesota lakes larger than 6000 ha for more than 40 yr, although the abundance of northern pike has varied (MN DNR files). On the other hand, the addition or removal of pike in smaller lakes (e.g. Heming Lake, Manitoba, and Grace, Horseshoe, and Harriet lakes, Minnesota) resulted in substantial changes in abundance of percids.

Cool-Water Fish Communities

Moyle et al. (1948) described three classes of lakes in Minnesota in terms of the abundance of perch versus the abundance of walleye and pike in standard gillnet catches. Our review of case histories and management implications illustrates some of the factors which are controlling the characteristics of these types of fish communities (Table 2). The addition of northern pike to Horseshoe and Grace lakes and their removal from Harriet and Heming lakes changed the degree of predation on perch and hence abundance of perch in these lakes. The abundance of white sucker was similarly affected in these lakes (white sucker not present in Horseshoe Lake). The abundance of yellow perch increased, but the abundances of white sucker and northern pike have not changed to date in Henderson and Savanne lakes, following removal of 89% and approximately 27% of the walleye population, respectively.

The degree to which northern pike populations can regulate the abundance of perch and suckers in lakes appears to depend on pike population size. Northern pike recruitment, although, appears to be controlled by the amount of weedy habitat that is available to smaller pike (<41 cm) as a refugium from cannibalism (Grimm 1983).

There is no clear relationship between the abundances of northern pike and walleye in lakes as would be expected from a relationship based on direct competition and predation. Self-regulation of pike populations at a level of abundance based on the area of weedy habitat undoubtedly contributes towards this. In addition, prey size selection curves for pike, sander (Popova 1982), and walleye (Parsons 1971) suggest that pike generally eat larger prey items than piscivorous percids. Northern pike consumed larger yellow perch than did walleye in Wilson Lake (Johnson 1977). The relationship of walleye and white sucker is primarily competition for benthos, while the northern pike – white sucker relationship is predation. Walleye is both a predator on and competitor with yellow perch and more of a competitor with white sucker. Northern pike appear to influence white sucker abundance more than do walleye.

The dynamics of white sucker populations suggest that, in the absence of a large northern pike population, they are largely self-regulating. Removal experiments with white suckers were generally followed by recovery to previous population abundances (this study; Olson 1963). Microcrustaceans are important in the diet of small suckers (Olsen 1963). Once beyond this life history stage, all size groups of white sucker compete for a common forage base (Olsen 1963; Johnson 1977); hence, intraspecific competition must regulate recruitment. Their efficiency in benthos foraging may allow them to outcompete benthic food resources from percids (Roff 1986).

Yellow perch populations in isolation display patterns of population dynamics which are relevant to an understanding of perch populations in complex communities. Diet generally changes with increasing fish size as European perch (*Perca fluviatilis*) shift from predation on zooplankton to benthos, and then to fish (Thorpe 1977; Popova and Sytina 1977). In perch-only lakes of the Soviet Union, there is a 17-yr cycle of population size structure in which successful year classes pass through these life history stages and then suppress subsequent year classes by cannibalism (Menshutkin 1971; Popova and Sytina 1977). A similar pattern is suspected to occur in Finnish lakes where only single year classes have been found (Sumari 1971).

In more complex communities, yellow perch abundance seems to be strongly affected by competition, particularly with white suckers for benthos (Johnson 1977). The growth rate response of yellow perch after sucker removal was restricted to larger fish (>100 mm; F. H. Johnson 1975). Roff (1986) suggested that suckers maintain a competitive advantage over yellow perch because mud-dwelling invertebrates, which are unavailable to fish hunting by vision, are vulnerable to the sucker's vacuuming approach. For continued high growth rate with age, yellow perch need to be able to access a succession of progressively larger food items according to growth efficiency models (Paloheimo and Dickie 1966; Kerr 1971; Kerr and Ryder 1977). The prey size changed in Wilson Lake because more mayflies were available to yellow perch after white sucker removal (Johnson 1977). Growth rates for European perch improved in a Swedish Lake when the degree of competition for zooplankton was reduced by removal of a large portion (40% of biomass, 70% of numbers) of the roach population (Persson 1986). Thus, a growth rate bottleneck occurring in the benthos feeding stage was removed as zooplankton became more available; consequently, young perch remained planktivorous for a longer period, reducing competition for benthos.

Cannibalism may be important in maintaining perch populations which contain large fish. Regier et al. (1969) suggested that the pattern of year classes in Lake Erie could be caused by cannibalism which suppressed subsequent year classes until the dominant year class was depleted by fishing. The importance of growth bottlenecks would be reduced if cannibalism controlled the density of young perch.

A consequence of improving the growth rate of intermediate-sized yellow perch will be an increase in recruitment of large perch because they are exposed to predation for less time. Empirical models of size-selective predation (Popova 1982; Parsons 1971) indicate that if yellow perch can reach a large size, they are relatively invulnerable to predation. Frost (1954) found that European perch larger than 15 cm experienced little predation in Lake Windermere. The lag in response of yellow perch abundance to pike stocking in Grace Lake apparently suggests that northern pike predation reduced the recruitment of yellow perch rather than directly affecting the abundance of large perch. A slow growth rate at intermediate sizes when perch are still vulnerable to predation creates a bottleneck limiting recruitment to large sizes. Werner and Gilliam (1984) have found numerous examples of this phenomenon.

Our review of lake histories and ecological relationships suggests that perch population dynamics are most appropriately

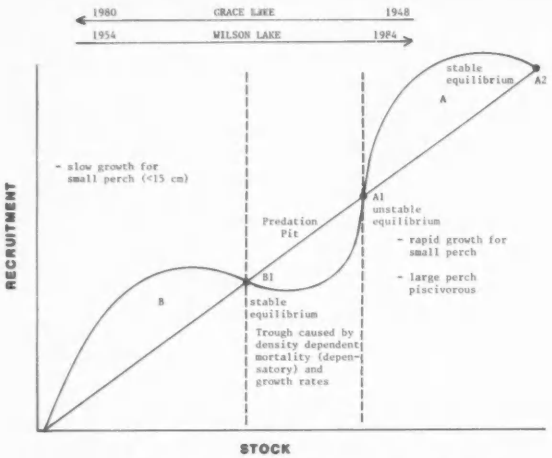

FIG. 13. Probable nature of the stock and recruitment relationship for yellow perch populations. In region A, a large stock is maintained by piscivorous feeding including cannibalism. If abundance is reduced to A1, density-dependent mortality affects survival of prerecruits (whose abundance is less due to lower population fecundity and survival) and the population shifts to a lower region of abundance (B). The population is maintained in B by lower population fecundity and the predation pit (Peterman et al. 1979). Cannibalisim is important in maintaining biomass in region A. While density-dependent mortality depends on contagious attack, the efficiency of predation is lowered at high levels of prey abundance (Holling 1973). The schooling habit of perch infers that predation behaviour is of the contagious attack form.

described by a model of stock and recruitment which incorporates depensatory mortality. Our proposal is a slight variation on the model of Peterman (1977) and Peterman et al. (1979). The latter suggested that populations can exist at two levels of abundance which are separated by a region of change, which they labeled a predation pit (Fig. 13). If the population size falls below A1, it drops all the way to region B and cannot return to region A. Our deviation from Peterman's (1977) model lies in noting the importance of perch growth rates in modifying the effect of predation on recruitment. We also suggest that maintenance of the larger stock (A) depends on cannibalism.

In combination, these arguments suggest that perch populations in the types of lakes that we examined tend to exist in one of two states (Fig. 13) which are characterized by the abundance of large piscivorous perch. In the low-abundance mode (Area B), the population is primarily controlled by competition with white suckers and walleye. Walleye and yellow perch exhibit a recruitment bottleneck because growth is affected by competition with suckers for benthic invertebrates, and the availability of YOY perch as forage is low because of low perch population fecundity. When large yellow perch are abundant (Area A), perch growth rates remain high because cannibalism apparently keeps the density of young perch low in spite of a high population fecundity. Small yellow perch (<12 cm) consumed large numbers of YOY perch in West Blue Lake (Kelso and Ward 1977). This suggests that if population fecundity is large enough, the dependence of yellow perch on benthos may be substantially reduced. Movement from B to A apparently requires removal of recruitment bottlenecks caused by the effect of competition on growth rates.

Discussion

The effects of removals on fish community structure are often given superficial consideration and, even when considered successful, have usually provided surprises. The removal of suckers from Wilson Lake, Minnesota, ultimately benefited walleye as intended, but the positive response of yellow perch was not predicted. In Dumbbell Lake, Minnesota, food made available through sucker removal was apparently diverted through rock bass rather than yellow perch, while in Big Bear Lake, Michigan, both perch and rock bass increased in abundance (Schneider and Crowe 1980). The response of perch to northern pike removal from Harriet Lake, Minnesota, was not anticipated but resulted in a prey base that allowed the establishment of walleye.

Sport fishing is the most pervasive form of fish removal. The effects of angling on the size/age structure of fish populations are well documented (Johnson and Johnson 1971; Goedde and Coble 1981; Osborn and Schupp 1985). Our model of yellow perch in coolwater communities (Fig. 13) suggests that reductions in the abundance of piscivores may allow perch and likely sucker populations to increase to a level where they control walleye abundance by competition. Our coldwater community model (Fig. 5) suggests that reductions in the abundance of large trout may similarly allow cisco abundance to increase and size composition to change. The net effect of this is increased competition with small lake trout depressing their growth rates.

A number of case histories have been described where management implications or unexpected perturbations caused a number of population responses (Tables 1 and 2), which we believe have aided us in better understanding mechanisms controlling interactions and interpreting community changes.

In disturbed communities that have not been invaded by new species, there is some evidence of return toward earlier states. White suckers in Wilson Lake have recovered to levels approaching those before removal, and the abundance of yellow perch has recently declined. The community structure in Horseshoe Lake showed signs of return to earlier conditions following relief from the predatory pressures of northern pike. Also, the Sallie Lake community appears to be reverting to a structure similar to that present before the most extreme disruption of the community. However, there is no evidence after 12–18 yr that these communities have or will reach their original equilibria. Fishery managers must be aware that processes which alter community metabolism are difficult if not impossible to reverse once in operation.

Because few studies of resource partitioning have been conducted on the Great Lakes (Brandt et al. 1980; Crowder et al. 1981), we believe that we must continue to obtain many of our insights from smaller lakes and other systems. Systems other than the Great Lakes provide replicates in space rather than time and accelerate our understanding of complex systems where responses to perturbations may take decades. We believe that our approach of studying interactions in numerous smaller systems and making allowances for spatial and temporal differences will accelerate our understanding of species interactions in the Great Lakes. For example, a diet composed of coregonids seemed to be important for walleye to achieve larger sizes and to maintain higher growth rates at larger sizes in Savanne Lake and Lac des Mille Lacs, Ontario. If coregonids enhance walleye growth, as suggested in Savanne Lake and Lac des Mille Lacs, then their abundance in Lake Erie may explain

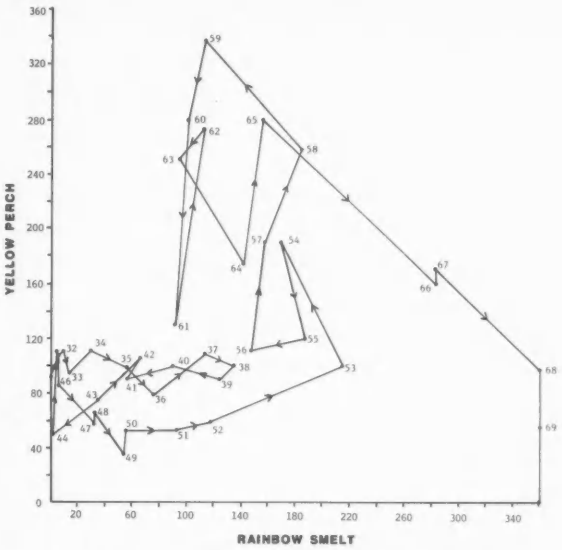

FIG. 14. Phase diagram of the relationship between abundances of adult stocks of yellow perch and rainbow smelt. The data for successive years are connected in the figure in order to indicate the chronology of changes in the relationship. The estimates were calculated from commercial catch data representing 1929–71 by Walter and Hoagman (1975) and using their abundance values as a percent of the 1929–43 mean.

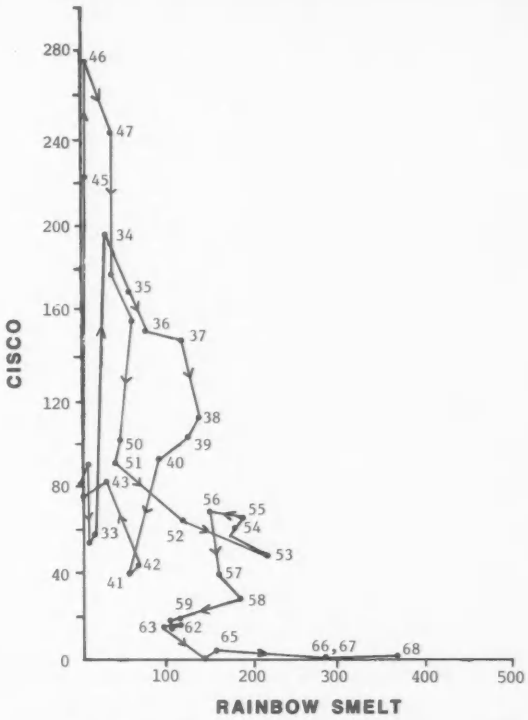

FIG. 15. Phase diagram of the relationship between abundances of adult stocks of cisco and rainbow smelt. The data for successive years are connected in the figure in order to indicate the chronology of changes in the relationship. The estimates were calculated from commercial catch data representing 1929–71 by Walter and Hoagman (1975) and using their abundance values as a percent of the 1929–43 mean.

in part why blue pike (*Stizostedion vitreum glaucum*) weighing 6.8–9.1 kg were not too uncommon prior to 1880 (Sterling 1884). The declining cisco population (a likely source of food for blue pike) and heavy fishing pressure might also explain why blue pike in the Michigan–Ohio waters (Baldwin and Saalfeld 1962) seldom exceeded 0.45 kg and rarely reached 2.3 kg in the early 1920's (Adamstone 1922). It is interesting to note also that blue pike commercial harvests began to oscillate regularly (1925–60) following the demise of cisco in Lake Erie (Baldwin and Saalfeld 1962). Regier et al. (1969) attributed much of this oscillation to cannibalism. The presence of cisco in Lake Erie at the turn of the century may have prevented intense cannibalism among blue pike.

The phenomenon of multiple equilibrium domains (Fig. 13) expressed by yellow perch populations in smaller inland lakes also occurs in the Great Lakes (Colby 1984). Suppression of yellow perch populations in southern Lake Michigan (McCormish 1981) is due to possible negative interactions with alewives and bloaters and in northeastern Lake Ontario (O'Gorman 1982) due to interactions with alewives.

A phase diagram (Fig. 14) using Green Bay data (Walter and Hoagman 1975) suggests that rainbow smelt had little influence on yellow perch there, since yellow perch increased steadily following the decline of cisco until the explosive increase of the alewife population in the 1960's. Thus, it appears at least in the Michigan sector of Green Bay that rainbow smelt have a greater negative relationship with cisco (Fig. 15) than with yellow perch (Fig. 14). Also, yellow perch seem to have a strong negative relationship with alewives, but can co-exist quite well with rainbow smelt, at least in large lakes. Walter and Hoagman (1975) found suckers (mostly white suckers) to be quite stable in northern Green Bay, similar to some of our smaller inland lake studies. Interestingly, Hoagman (1973) concluded that alewives do not appreciably affect whitefish year class strength, but may be beneficial to whitefish by reducing the abundance of competitor and/or predator species.

The uncertainty of predicting the outcome of manipulative studies or management strategies suggests to us the immediate need to better organize our collective observations of community responses to disturbances or the more stressful perturbations and expand our research and management (operations) efforts towards conducting well-designed manipulative studies in the field. As we better understand the sequential community interactions as they relate to habitat and respond to known disturbances, fishery science should rapidly advance to the predictive capabilities desired by most managers.

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Increased Catchability of the Deep Monofilament Nylon Gillnet and Its Expression in a Simulated Fishery[1]

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Collins, J. J. 1987. Increased catchability of the deep monofilament nylon gillnet and its expression in a simulated fishery. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 129–135.

During 1979–81, Lake Huron fishermen changed from using 36-mesh monofilament nets to deeper (50-mesh) nets in the commercial fishery for lake whitefish (*Coregonus clupeaformis*). Simultaneous catch comparisons between the two gears showed that overall, deep nets were 1.7 times more efficient (but varied seasonally) for whitefish. The increase in efficiency exceeded that expected from the increase in area of the deeper nets. Simulation modeling demonstrates that the expression of enhanced catchability of deep nets is inversely proportional to the intensity of the fishery and thus total mortality rates (*Z*). Further, the temporal distribution of yield to the fishery would be advanced within the fishing period. This most recent change in catchability has introduced further bias in commercial catch and effort statistics.

Des 1979 à 1981, les pêcheurs commerciaux de corégones de lac (*Coregonus clupeaformis*) du lac Huron ont délaissé les filets en monofilament de taille de maille 36 pour des filets plus hauts de taille de maille 50. La comparaison des taux de prises simultanés des deux types d'engins a montré que, de façon générale, les filets plus hauts étaient de 1,7 fois plus efficaces pour la capture du corégone, bien que les résultats variaient selon la saison. L'accroissement d'efficacité était supérieur à celui qui devait découler de la surface plus grande des filets plus hauts. Une modélisation par simulation a permis de montrer que la plus grande capacité de prises des filets plus hauts était inversement proportionnelle à l'intensité de la pêche et donc au taux de mortalité total (*Z*). De plus, la distribution temporelle du rendement de la pêche devrait être avancée au sein de la saison de pêche. Cette modification très récente de la capacité de prises introduit un autre biais dans les statistiques sur les prises et l'effort de la pêche commerciale.

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This paper quantifies, by comparison netting, the change in efficiency resulting from an increase in the depth of monofilament nylon gillnets (from 36 meshes to 50 meshes) currently used in the Lake Huron commerical fishery for lake whitefish (*Coregonus clupeaformis*).

The use of deeper nets during the late 1970s is the most recent change in the historical development of the gillnet fishery. Cotton and linen netting materials were used before 1950 and nets were usually 18–24 meshes deep. The cotton was replaced by multifilament nylon web (and sidelines) in the early 1950s with a reported threefold increase in catching power for whitefish (experimental net comparisons (McCombie and Fry 1960)). During the 1960s, fisheries began using nylon nets that were 30–36 meshes deep, but this gear change was not evaluated. Catching power for whitefish was further increased by about 1.8 times with the introduction of monofilament nylon twine during the early 1970s (Collins 1979). This new gear was also shown by experimental net comparisons to be more efficient for certain Pacific salmon (*Oncorhynchus* spp.) (Larkins 1963, 1964; Washington 1973) and other marine species (Pristas and Trent 1977).

To examine the relative efficiency of deep nets for whitefish and associated species, both deep and shallow nets were fished simultaneously on three stocks of whitefish in northern Lake Huron. Differences in fish size selectivity and the catchability of the two gears were assessed. Computer simulation models were developed to demonstrate how the improved catchability of deeper nets may be expressed in a fishery.

Materials and Methods

Test nets were 121-mm mesh (stretched measure) and were constructed to replicate commercial nets used during 1979 to catch whitefish in the North Channel. It should be noted that mesh sizes employed by the fishery ranged from 114 to 127 mm but the former was more common in Lake Huron proper. The nominal filament diameter of the monofilament web was 0.23 mm and the hanging ratio was 0.46 (50:108 m), that is 108 m of stretched webbing was hung on 50 m of sideline (for a description of hanging ratios, see Garner 1962; Lusyne 1959; Christie 1978).

Each net panel was 91.4 m long and the deep nets (50 meshes) were an estimated 5.7 m deep from lead line to cork line, while the shallow nets (36 meshes) were about 4.1 m deep. As in commercial nets, sidelines extended beyond the webbing at the ends of each panel to provide attachment to adjacent nets. Therefore when panels were joined together to form a gang, there was an unwebbed space of about 1 m between each panel.

The relative efficiency of the two gear types was compared by

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combining the panels into an experimental gang of nets which was 731 m long. It consisted of eight (91.4 m) nets joined together in a string of alternating panels in a repeated deep–shallow–deep–shallow configuration.

All sets were made on the lake bottom at depths frequented by whitefish which range from shallow waters in the spring and fall to 58 m during the summer months. Therefore in the majority of sets the cork lines of the nets were from 2 to 50 m below the lake surface. As in a normal commercial operation, nets were usually set in the afternoon and lifted the following morning (fishing overnight for a period of about 18 h).

During 1979, the gang was set 63 times (a total effort of 46 km of net) in the two basins of South Bay, Lake Huron (45° 38′ N, 81°52′ W). Each basin harbours a discrete stock of whitefish, having different growth parameters and thus different recruitment ages (Collins 1979).

A second series of netting trials was conducted during 1980 on another discrete whitefish stock (Casselman et al. 1981) in the North Channel of Lake Huron (46° 05′ N, 83° 00′ W). The experimental gang was incorporated into a commercial fisherman's string of nets (50 meshes deep) which averaged 2100 m in length. The fisherman made 72 sets (in total, 52 km of net lifted) for whitefish during the May–November period. In both tests, deep and shallow net catches were examined separately. The number of each species caught and the fork length and weight of each whitefish taken were recorded. The set location, duration, depth, and water temperature were also recorded for each netting trial. The relative catch rate of the two gears is expressed as the ratio obtained by dividing either deep net catch values by shallow net catches when effort is equal or deep net CUE by shallow net CUE, where CUE equals the number of fish caught per kilometre of net set for one night.

Deep and shallow net catches were compared statistically by applying a Wilcoxon's signed-ranks test for paired observations (Sokal and Rohlf 1969, p. 400). The null hypothesis that the two gears caught equal numbers of fish was rejected if the computed value had a probability <0.05. This test was also applied after the shallow net catches were increased by a factor of 1.39 to compensate for the smaller area of the shallow nets.

The null hypothesis that the length–frequency distributions of fish from both gears were the same was examined by a chi-square test for independence using $2 \times k$ contingency tables.

Models and Their Parameters

Analytical Model

The basic properties of the test netting results can be examined by using a very simple analytical model derived directly from Baranov's catch equation. If it is assumed that catchability is dependent solely upon gear type, then the catch rates for deep and shallow gears can be written as follows:

$$(1)\quad \frac{C_D}{C_S} = \frac{[q_D E/(M + q_D E)]\cdot(1 - e^{-M-q_D E})\cdot N}{[q_S E/(M + q_S E)]\cdot(1 - e^{-M-q_S E})\cdot N}$$

where E = effort which is the same for deep and shallow nets, q_S = the catchability of shallow nets, $q_D = \zeta \cdot q_S$ = catchability of deep nets where ζ is the efficiency factor assumed to be equal to 1.7, M = natural mortality rate, assumed constant at 0.4234 for all age-classes, C_D = catch by deep nets if population size = N and effort = E, and C_S = catch by shallow nets if population size = N and effort = E.

This simplifies to

$$(2)\quad \frac{C_D}{C_S} = \zeta \frac{M + q_S E}{M + \zeta q_S E} \cdot \frac{(1 - e^{-M-\zeta q_S E})}{(1 - e^{-M-q_S E})}$$

which is approximately equal to ζ when E is close to zero. Therefore, with low effort the catch ratio would be expected to equal the efficiency factor, ζ. As effort increases, equation 2 demonstrates that the value of the catch ratio will drop further and further below ζ.

Simulation Models

The analytical results outlined above hold for a very simplified fishery where catchability is assumed to be independent of both the age structure and population abundance. Simulation models were used to illustrate how the analytical results would be affected by including both fish size structure and density-dependent effects on the catchability coefficient (q).

Scenarios were run with q assumed to be constant and with q inversely related to abundance. There is growing evidence that the latter assumption applies to gillnet catchability (Henderson et al. 1983; Winters and Wheeler 1980). Bi-daily fishing effort is constant (another simplification) and net selectivity for 114-mm-mesh nets is used because this mesh size is most commonly employed in Lake Huron fisheries. Further, a selectivity curve for 114-mm mesh (but not for 127-mm mesh) has been published (Regier and Robson 1966). Whitefish growth is assumed to be an average of size at age curves for North Channel whitefish data (Spangler and Collins 1980). Changes in growth and selectivity parameters would yield different quantitative results from those presented in this paper.

Two deterministic models (A and B) were written in Applesoft Basic to simulate the effect of improved gear catchability on yield from a hypothetical whitefish stock during a single fishing season. The simulation time step was 2 days and there were 100 time steps representing a fishing period from May to November. Output from the model includes the temporal distribution of yield to a size-selective gillnet fishery and the size and age structure of the catch and survivors at the end of the fishing season. Models A and B differ in that in model A, all members of a particular age-class in the population (although growing) have the same lengths at a given time step whereas in model B, each age-class has a length distribution. Model B simulations were run for one age-class at a time and the results were summed to represent the entire stock. All scenarios were run with catchability coefficients adjusted to represent deep and shallow net fisheries.

Fishing Component of Model

Instantaneous fishing mortality (F) is determined by the relation

$$F = E \cdot q \cdot \mathrm{NS}_i$$

where E is effort (in kilometres of net set per 2 days), q is the catchability coefficient which is set at 1.4354×10^{-4} for shallow nets (and 1.7 times greater for deep nets) and represents the proportion of the vulnerable stock (VS) taken by 1 km of net set (in scenarios where q was density dependent, it was assumed to be inversely proportional to the vulnerable stock by the relation $q = 0.231\mathrm{VS}^{-0.5745}$), and NS_i is net selectivity coefficient for fish size-class i, based on the size selectivity curve for 114-mm-mesh (stretched measure) gillnets (Regier

TABLE 1. Number of fish caught in 50-mesh nets (D) and 36-mesh nets (S) with 26.0 km of each net type set in the North Channel, 12.8 km in South Bay (outer basin), and 10.2 km in the inner basin. Catch ratio values = D/S.

Species	North Channel			South Bay (outer basin)			South Bay (inner basin)			Grand total		
	D	S	Ratio	D	S	Ratio	D	S	Ratio	D	S	Ratio
Lake whitefish	1176	711	1.7	347	179	1.9	267	173	1.5	1790	1063	1.68
White sucker	785	578	1.4	56	83	0.7	15	10	1.6	856	671	1.28
Longnose sucker	418	286	1.5	2	3	0.7	—	—	—	420	289	1.45
Rainbow smelt	98	68	1.4	19	12	1.6	187	124	1.5	304	204	1.49
Alewife	30	33	0.9	26	15	1.7	5	3	1.7	61	51	1.20
Lake trout	9	6	1.5	3	1	3.0	32	21	1.5	44	28	1.57
Splake (backcross)	—	—	—	24	11	2.2	14	10	1.4	38	21	1.73
Others[a]	64	44	1.5	24	9	2.7	13	10	1.3	101	63	1.60

[a]Principal genera and their D/S ratios were *Esox* (1.8), *Lota* (1.4), *Stizostedion* (1.7), *Coregonus* (1.5), *Prosopium* (1.4), and *Acipenser* (2.5).

and Robson 1966); it determines the number of fish at each size that are vulnerable to the nets.

The catch (C_i) for each size-class (i) is determined using Baranov's catch equation (Ricker 1975, p. 13) in which F and instantaneous natural mortality (M) occur simultaneously:

$$C_i = N_i \cdot (1 - \exp(-F_i + M)) \cdot (F_i)/(F_i + M)$$

where N_i is the number of fish in size-class i. Catches by age-classes were determined in a similar manner.

Biological Parameters

The instantaneous natural mortality rate (M) was the same for all fish in the population and was fixed in the model at 0.00232 for each bi-daily time step. This rate is equivalent to the annual conditional mortality of 34.5% estimated for whitefish by Cucin and Regier (1966). Growth was not density dependent and was assumed to occur during the 200-d fishing season. Fish lengths (centimetres) at the beginning of the season were related to age in years by the following regression:

$$L = 19.598 + 17.523 \log_e \text{age}$$

and fish weights (kilograms) were assumed to be related to fork length (centimetres) as follows:

$$W = 8.1505 \times 10^{-6} \cdot L^{3.1350}.$$

Fork length by age and weight at the beginning of the season and the instantaneous growth rates (G) of each age-class during the season were as follows:

Age (yr)	Fork length (cm)	Weight (kg)	G ($\times 10^{-3} \cdot d^{-1}$)
2	31.9	0.42	1.01
3	38.8	0.78	0.62
4	43.9	1.15	0.43
5	47.8	1.50	0.32
6	51.0	1.84	0.26
7	53.7	2.16	0.21
8	56.0	2.47	0.18
9	58.1	2.77	0.15
10	59.9	3.05	0.10

In model B, each age-class was assigned an initial length distribution comprising 10 length-classes. An assumed population of 200 000 age 2 fish with a normal distribution of lengths (mode 31 cm, range 26–35 cm) and the appropriate G was run through the model and the survivors became the initial population of age 3 fish. By running each subsequent age-class through the model, the initial size and age composition and the number of fish in the population were simulated. It reflected the effect of each age-class having passed through a size-selective gillnet fishery in the previous season. The resulting composite structure (size and age) of the population is analogous to one having constant recruitment and fishing pressure over a period of 10 yr, a hypothetical situation.

Results

Empirical Catch Comparisons

Numbers and species of fish caught (Table 1) in the experimental nets were typical of whitefish fisheries in the areas netted. Lake whitefish dominated the catches, but associated species white sucker (*Catostomus commersoni*) and longnose sucker (*C. catostomus*) were also numerous, particularly in the North Channel. Small catches of lake trout (*Salvelinus namaycush*) and splake backcross (*S. namaycush* × *S. fontinalis* × S. *namaycush*) in South Bay represent recruitment of fish being stocked there. The two small species, rainbow smelt (*Osmerus mordax*) and alewife (*Alosa pseudoharengus*), were caught only by entanglement of their mouth parts in the web.

Overall, deep (50-mesh) nets were 1.7 times more efficient than shallow (36-mesh) nets for catching whitefish (Wilcoxon's signed-ranks test, $P < 0.001$). Deep nets also appeared superior for catching the other species encountered. Whitefish catches in deep nets were significantly greater for most months, but deep/shallow net catch ratios varied during the fishing season (Table 2). Apart from being highest during May in both areas, there was no consistent seasonal trend in catch ratios. Whitefish catches by deep nets relative to shallow nets increased more than would be expected on the basis of the increased area (39%) of deep nets alone. When all shallow net catches were multiplied by a factor of 1.39, to correct for area differences between the two gear types (Table 3), deep net catches were still significantly larger overall ($P < 0.001$).

There were no significant correlations ($P > 0.05$) between deep/shallow catch ratios and water temperatures, depth of sets, or abundance of fish (CUE).

Net Selectivity for Size

Modal length-classes of whitefish from both gears were the same for the North Channel catches (Fig. 1). Although

TABLE 2. Seasonal variation in effort, depth of sets, and catches of whitefish in deep 50-mesh nets (D) and shallow 36-mesh nets (S), where CUE equals fish per kilometre of net lifted. P is the probability value from the Wilcoxon's signed-ranks test used to compare catches from the two types of nets.

	North Channel (1980)						South Bay (1979)[b]					
		Mean	CUE					Mean	CUE			
Month	Effort[a]	depth (m)	D	S	D/S ratio	P	Effort	depth (m)	D	S	D/S ratio	P
May	2.47	5.2	14.6	5.7	2.56	<0.05	2.56	12.3	43.4	19.5	2.22	<0.01
June	7.32	10.6	22.3	13.7	1.63	<0.002	3.29	20.2	17.3	12.5	1.39	>0.05
July	5.49	15.9	29.9	19.7	1.52	<0.001	2.56	40.1	28.9	13.8	2.18	<0.01
August	4.75	17.1	35.5	23.6	1.5	<0.05	2.93	46.7	32.1	19.8	1.62	<0.01
September	1.28	21.7	25.0	10.2	2.50	—	3.29	37.7	15.5	12.1	1.28	>0.05
October	6.95	9.1	25.9	14.4	1.80	<0.05	5.85	17.1	10.4	5.3	1.97	<0.01
November	3.29	3.4	131.2	79.9	1.64	<0.01	2.56	14.4	64.5	37.5	1.72	<0.05
Overall	31.55	11.73	37.27	22.5	1.66	<0.001	23.04	25.9	26.6	15.2	1.75	<0.01

[a]Kilometres of each gear type lifted; effort doubled for two night sets in the North Channel.
[b]Inner and outer basin data combined.

length–frequency distributions for deep and shallow nets fished in South Bay were similar, deep nets tended to catch smaller fish (modal length class 42–44 cm) than shallow nets (modal length class 44–46 cm). However, this difference was only significant in outer basin catches (chi-square test on numbers of fish, $P < 0.01$). For deep and shallow net catches combined, South Bay fish (modal length 44 cm) were smaller (χ^2, $P < 0.05$) than those from the North Channel (mode 46 cm).

The size of fish retained most efficiently by gillnets increases as mesh size increases and 114-mm-mesh nets are estimated to be most efficient for 45-cm whitefish as shown in fig. 9 of Regier and Robson (1966). Judging by inspection of that figure, 121-mm-mesh nets used in this study would be most efficient for whitefish in the 46- to 48-cm length stratum. Therefore, most of the fish taken, particularly those in South Bay, were suboptimal in size and were recruiting to the gear.

Regarding age structure of the catches, age 4 fish dominated in the North Channel (53% of the total catch) and in the outer basin of South Bay (57%). In contrast, 11-yr-olds dominated inner basin catches (30.6%), reflecting the slow growth rate of that discrete stock (Collins 1979).

Computer Simulations

Scenarios run to determine deep net (D) and shallow net (S) catch ratios at various effort levels (and thus levels of total mortality (Z)) show that the D/S ratio is inversely related to Z in the shallow net fishery (Fig. 2). Therefore at low effort levels, as in experimental netting, the improved catchability of the deep net is fully expressed, yielding a 1.7-fold increase in catch with a change to deep nets. However, when the shallow net fishery is intense ($Z = 1.4$), catches resulting from a change to deep nets would be about 1.3 times greater, much less than indicated by the experimental netting study.

The analytical result (equation 2 when $M = 0.4234$ and $\zeta = 1.7$) (solid line, Fig. 2) represents a much simplified situation, but lies very close to simulation model A which assumes that all fish in an age-class are the same size. When a population with size-structured age-classes is included in the model, the increase in catch with a change to a more efficient gear is less than that predicted by the analytical model.

Although the increased catchability of deep nets may result in larger catches (depending upon Z), a greater proportion of the fish would be taken earlier in the season. This is true even for age 3 fish which are small and recruiting to the gear throughout the fishing season (Fig. 3A). Furthermore, catches of older (and larger) fish (other than fall-spawning stocks) would be greatest at the beginning of the fishing season because, as the season progresses, they grow beyond the peak size-selective efficiency of the nets (Fig 3B).

TABLE 3. CUE's of whitefish (data from all areas combined) with shallow net catches corrected ($S_c = S \times 1.39$) to equate them to the area of deep nets. P is the probability value from the Wilcoxon's signed-ranks test used to compare catches from the two types of nets.

	Total effort[a]	CUE		D/S_c ratio	P	No. of paired sets
		D	S_c			
May	5.03	29.2	17.7	1.65	<0.001	13
June	10.61	20.7	18.5	1.12	>0.05	26
July	8.05	29.6	24.7	1.20	<0.02	21
August	7.68	34.2	30.7	1.11	>0.05	18
September	4.57	18.2	16.1	1.13	>0.05	13
October	12.80	18.8	14.2	1.32	>0.05	30
November	5.85	102.0	85.3	1.20	<0.002	14
Overall	54.59	32.8	27.0	1.21	<0.001	135

[a]Kilometres of each gear lifted; effort doubled for two night sets.

Size Composition of the Simulated Catch

The modes in the size distribution of fish taken by 114-mm-mesh gillnets were 41 and 43 cm for both deep and shallow nets, assuming a stock size composition depicted in Fig. 4. Clearly, since these modes lie below the optimum size (45-cm length stratum) of fish selected by 114-mm nets, most fish were being caught as they recruited to the gear. Additional simulations demonstrated that as fishing mortality increased the modal length-class shifted further left of the optimum size. In an intense fishing scenario ($Z = 1.8$) the mode of the size composition of the catch was at 42 cm.

The size composition of the surviving population (dotted line, Fig. 4) is dominated by a peak at the 39-cm interval. This peak represents 2-yr-olds which have grown throughout the fishing period. About 82% of fish < 41 cm long belong to this age-

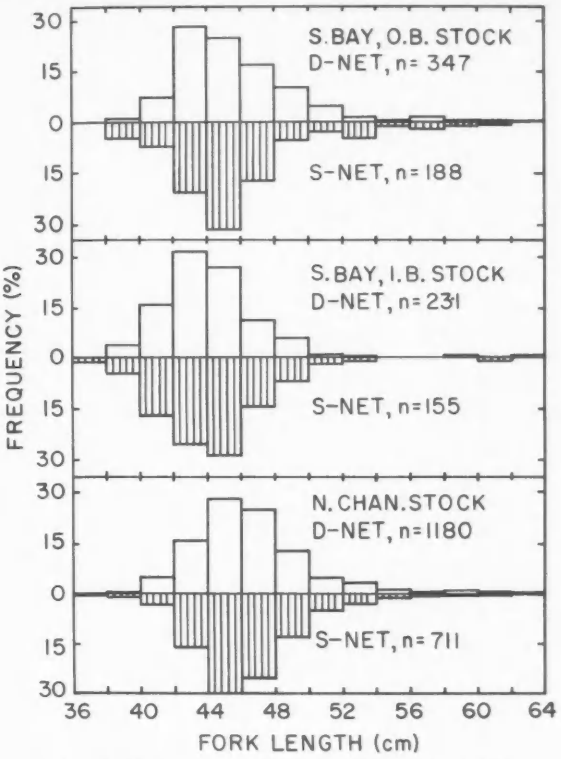

FIG. 1. Length–frequency distributions of whitefish taken in 121-mm mesh deep and shallow gillnets in South Bay (1979) and the North Channel (1980) of Lake Huron.

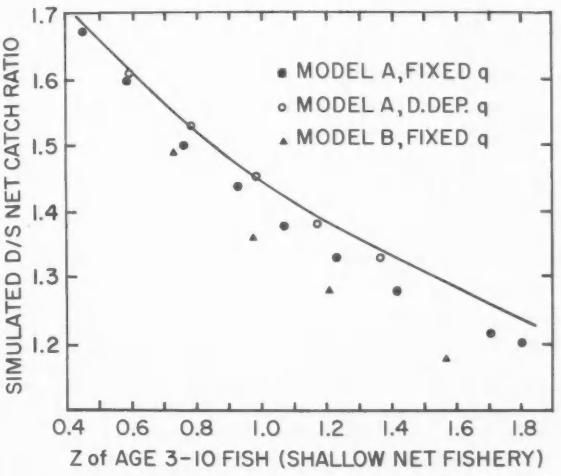

FIG. 2. Result of analytical equation 2 where $M = 0.4234$ and $\zeta = 1.7$ (solid line) and simulated D/S net catch ratios (model A) resulting from various levels of fishing effort applied equally to a given population. Solid circles represent scenarios with fixed q and open circles those with density-dependent q. Solid triangles show results of model B scenarios.

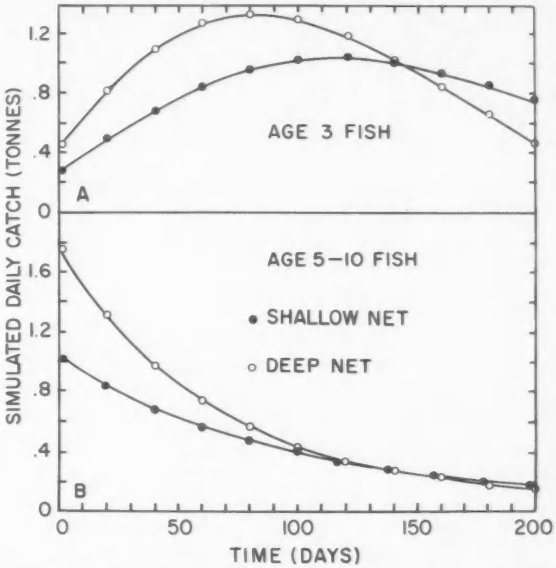

FIG. 3. Simulated temporal distribution of yields (model A) in shallow and deep nets with equal effort of each gear applied on the same initial population. (A) Age 3 fish; (B) combined catches of age 5 and older fish.

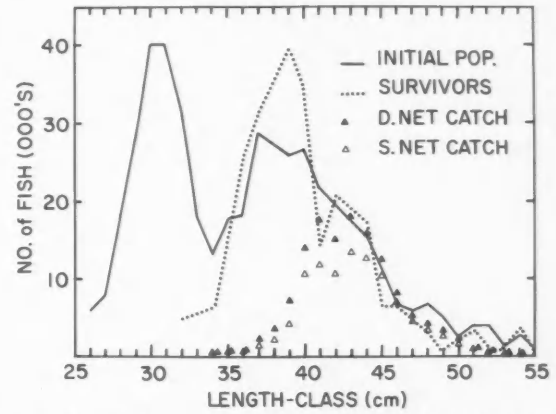

FIG. 4. Simulated size-structured population (model B) initially (solid line), after fishing with shallow nets (dotted line), and the size composition of the catch (open triangles). The deep net catch with the same effort is shown by solid triangles.

class. Assuming recruitment of 1-yr-olds (not depicted here), the surviving population would also have a second peak at 31 cm, similar to the initial population structure.

Discussion

This comparison of nets has shown overall that deep (50-mesh) nets catch about 1.7 times more whitefish than shallow (36-mesh) nets, but the D/S catch ratio varied seasonally. Similar unexplained variations have been recorded in other net comparison studies (Washington 1973; Collins 1979).

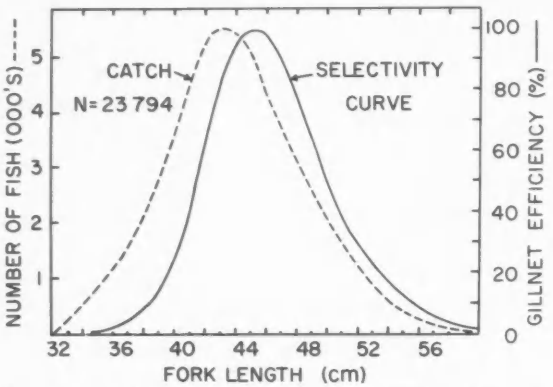

FIG. 5. Length–frequency distribution of whitefish in North Channel commercial gillnets (1958–74 data) (broken line) compared with the selectivity curve for 114-mm-mesh gillnets used in the simulation model (solid line)(redrawn from Regier and Robson 1966).

By 1979 many commercial fishermen had recognized the greater efficiency of deep nets by comparing catches in this new gear set along with their normal nets. The fishery has readily adopted new fishing gear several times since 1950, changing from cotton to multifilament nylon gillnets (McCombie and Fry 1960), from 24-mesh to 36-mesh nets, and from multifilament nylon to monofilament nylon web (Collins 1979). Each gear change was adopted because increased efficiency could be observed directly by comparing catches in the gear types.

While catchability has undoubtedly increased, the intrinsic efficiency of deep nets would not be expressed in increased yields unless total mortality rates were low. The inverse relationship between total mortality rates and apparent change in catchability (Fig. 2) may account for Hogman's (1973) failure to observe an increase in yield when the whitefish fishery of Green Bay, Lake Michigan, changed over from cotton to nylon gillnets.

During 1958–62, the North Channel whitefish stock experienced high mortality ($Z \sim 1.5$) due to combined commercial exploitation and sea lamprey (*Petromyzon marinus*) predation (Spangler and Collins 1980). Similarly, in the late 1960s total mortality was exceedingly high ($Z \sim 4.9$) for 4-yr-old whitefish at Burnt Island in northern Lake Huron (Spangler 1970). A change to deep nets during those periods (without increasing effort) would have increased yield (number of fish) by only about 27% in the North Channel and there would have been virtually no increase at Burnt Island (Fig. 2).

Simulation results illustrate that the modal length of fish caught in 114-mm mesh lies to the left of the mode in the selectivity ogive (Fig. 4). Christie (1978) observed this phenomenon in a Lake Ontario fishery. Empirical data on the length distribution of North Channel whitefish catches are consistent with the simulation result (Fig. 5) and indicate that during 1958–74 the fishery generally harvested fish that were recruiting to the gear. The length distributions of catches from this study (Fig. 1) show a similar relationship although the mesh size (121 mm) is larger.

The advanced temporal distribution of the catch (demonstrated by simulation, Fig. 3) is a logical result of increased gear efficiency. However, the regularity of the curves depicting catch is unrealistic because constant effort is assumed in the model. Of course, effort in a real fishery varies throughout the season in response to market forces and weather conditions. In principle, with increased catchability, catches would peak earlier in the fishing period and consequently the fish in the catch would tend to be smaller.

Management Implications

Assessment of stock abundance is often based on commercial catch and effort data when other indices are lacking. Average annual abundance is usually estimated by computing catch per unit of effort (CUE). Clearly, changes in gear catchability bias such estimates, and therefore, as suggested by Cucin and Regier (1966) and Collins (1979), effort units must be multiplied by an "efficiency factor" (1.7 in this case) to compensate for increased gear catchability.

Such improvements in catchability must be continually evaluated if management decisions are based on commercial catch statistics (Collins 1979). Christie (1978) reviewed fishery regulations in the Great Lakes which up to the late 1970s included licensing of the number of fishermen and units of effort, minimum mesh sizes, and minimum fish size in the catch. In the Lake Huron fisheries before 1984, neither the size of catch nor changes in gear efficiency (effective effort) were regulated. Therefore the several increases in gear efficiency which have occurred since 1950 in Lake Huron could have led to extreme exploitation pressure on certain stocks.

However, consistent with the new management strategy for Ontario fisheries (Loftus et al. 1978), allocation of resources to commercial fisheries, commencing in 1984, has been made on the basis of catch quotas assigned to individual fishermen by area. As suggested by Christie (1978), this procedure reduces competition. Under this new management strategy, it remains important to evaluate gear efficiency (for assessment purposes), but the negative effects of improved gear catchability are now controlled by an upper limit on yield to the fishery. A quota management system, however, requires greater precision in the assessment of stock abundance and the prediction of yields.

Acknowledgments

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Models on the Slope of, and Biomass Flow up, the Biomass Size Spectrum

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A comparison is made between the different models of the biomass size spectrum proposed by a number of authors. Though superficially dissimilar, the models are all mathematically compatible if the differences in their underlying assumptions are taken into account. The simplest model does not consider the complexities of food webs over food chains, somatic growth, or the continuous nature of the size spectrum. Comparison with the more complex models, however, shows that these omissions do not seriously affect the slope of the size spectrum. For example, one model predicts that the effects of somatic growth and reproduction cancel if cohort biomasses remain relatively constant as the cohorts mature. If growth rate is related to body size in an allometric relationship and reproduction is ignored, then another model gives a slightly different slope (higher by roughly 0.03). If the same assumptions are used in both models, however, they give compatible results. Some simple equations are suggested for routine application in size spectrum analysis of biomass and production data.

L'auteur compare différents modèles de gammes de tailles de biomasse proposés par divers chercheurs. Bien qu'apparemment différents, ces modèles sont tous mathématiquement compatibles si l'on tient compte des différences entre leurs hypothèses de départ. Le modèle le plus simple ne tient pas compte de la complexité des réseaux alimentaires par rapport aux chaînes alimentaires, de la croissance somatique ou de la nature continue de la gamme de tailles. La comparaison avec des modèles plus complexes montre cependant que ces omissions ne modifient pas de façon importante la pente de la gamme de tailles. Ainsi, un des modèles prévoit que les effets de la croissance somatique et de la reproduction s'annulent si les biomasses des cohortes demeurent relativement constantes à mesure que celles-ci maturent. Un modèle où le taux de croissance est relié à la taille corporelle par une relation allométrique et qui ignore la reproduction donne une pente légèrement différente (plus élevée d'environ 0,03). Les résultats sont cependant compatibles lorsque les mêmes hypothèses de départ sont utilisées avec chacun des modèles. L'auteur présente quelques équations simples d'application générale pour l'analyse par gamme de tailles des données de biomasse et de production.

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Organization and production of whole ecosystems are often difficult to describe and predict from relatively simple equations. In pelagic ecosystems, however, most consumers are considerably larger than their prey, and body size is therefore a rough indication of trophic level. Ecosystem structure can, therefore, be described in terms of a biomass size spectrum, and production can be defined in terms of biomass flow[1] up this size spectrum. For example, Sheldon et al. (1972) demonstrated that the biomass size spectrum (biomass over equal (on a logarithmic scale) size classes plotted against log body size) in the ocean is fairly flat (i.e. biomass within any size class W_x to W_y divided by log (W_y / W_x) is roughly constant). This fact was confirmed by Sheldon et al. (1977), who also developed a simple model, based on predator–prey size ratios and the efficiency of biomass conversion between trophic levels, to explain it. The structure of pelagic ecosystems is, however, more complex than a simple food chain, and several models have been developed to include various levels of complexity. Platt and Denman (1977, 1978) presented a model which considered biomass flow up the size spectrum as a continuous process, rather than transfer between discrete trophic levels. This model did not, however, specifically describe the process of predation. Silvert and Platt (1978, 1980) dealt with both somatic growth and predation in a continuous biomass flow model. Borgmann (1982) developed a procedure for dealing with food webs, as opposed to food chains, and Borgmann (1983) described how the effects of somatic growth and reproduction could affect efficiency of biomass flow up the pelagic ecosystem.

These models of the biomass size spectrum have several important applications. For example, they allow predictions of fish production from primary production (Sheldon et al. 1977) or zooplankton production (Borgmann et al. 1984), and

[1]Biomass flow, as used here, refers to movement of biomass from one size to another through somatic growth, predation, or reproduction. Units of dry weight are often the most convenient, although body volume, energy content, or elemental composition (e.g. carbon, nitrogen) may also be used. If tissue chemical composition (and hence also energy content per unit body mass) is similar at all trophic levels, then the slope of the size spectrum will be independent of the units used.

facilitate the estimation of fish mortality rates in the open ocean (Peterson and Wroblewski 1984). They also provide a means of modelling the flow of persistent contaminants up the food web, giving a theoretical basis for the use of allometric relationships between body size and contaminant concentrations (Borgmann and Whittle 1983). Superficially, the models of Sheldon et al., Platt and Denman, Silvert and Platt, and Borgmann appear different. They can be shown, however, to give the same results when the same underlying assumptions are used in each model. I will attempt here to briefly compare the different models and show why they give different slopes for the biomass size spectrum (i.e. which assumptions lead to different slopes). Some simple equations that can readily be applied to the analysis of biomass and production data are listed in Table 1. Their application is demonstrated in later papers presented in this issue (e.g. Minns et al. 1987; Leach et al. 1987).

A Simple Food Chain

The ratio of production at one trophic level (P_i) to production at the next (P_j) is a function of biomass conversion efficiency during growth and reproduction (K_1) and the proportion of the prey production consumed by the predator. For simplicity, all the prey production will be assumed to be consumed by the predator. If we relate production to the mean body size (mass) of the organisms in sequential trophic levels (W_i and W_j), we can write

$$\frac{P_j}{P_i} = K_1 = \left(\frac{W_j}{W_i}\right)^{-\epsilon}.$$

The exponent ϵ is found by rearrangement of the above equation and is equal to $-\log(K_1) / \log(W_j/W_i)$. If we assume that K_1 and the predator–prey size ratio (W_j/W_i) are relatively constant, we can relate production at trophic level i to production at level $i + u$ using

$$(1)\quad \frac{P_{i+u}}{P_i} = (K_1)^u = \left(\frac{W_j}{W_i}\right)^{-u-\epsilon} = \left(\frac{W_{i+u}}{W_i}\right)^{-\epsilon}.$$

Production at any trophic level can therefore be calculated from production at any other trophic level without taking into account the number of trophic levels involved directly, if ϵ is known. Borgmann (1982) called ϵ the particle-size-conversion efficiency because it is a measure of the efficiency of biomass conversion from one size to another, rather than one trophic level to another. If K_1 and the predator-prey size ratio are fairly constant, and if all prey production is consumed by each predator, then ϵ defines the slope of the production size spectrum. The product of production times W^{ϵ} at any trophic level is equivalent to the same product calculated at any other trophic level. This has been designated as F by Borgmann (1982) and represents a measure of the biomass flow up the food chain. Having calculated F at one trophic level, production at any other trophic level can be estimated from

$$(2)\quad P_i = FW_i^{-\epsilon}.$$

This equation can only be used to estimate production at other trophic levels if all prey production is consumed by the predator. Otherwise, equation 2 does not hold and F decreases at those trophic links where production is lost through pathways other than predation.

Defining a biomass size spectrum requires a relationship between growth rate (i.e. the production/biomass ratio) and body size. An allometric relationship is usually assumed where growth is given by aW^{-n}, where a and n are constants. Consequently, P_i is equal to $aW_i^{-n}B_i$ where B_i is the biomass of trophic level i. Substituting into equation 1 gives

$$(3)\quad \frac{B_{i+u}}{B_i} = (K_1)^u\left(\frac{W_{i+u}}{W_i}\right)^n = \left(\frac{W_{i+u}}{W_i}\right)^{n-\epsilon}.$$

Alternatively, substituting into equation 2 gives (Borgmann 1982)

$$(4)\quad B_i = (F/a)W_i^{n-\epsilon}.$$

The slope of the biomass size spectrum is therefore defined by $n - \epsilon$.

Sheldon et al. (1977) used essentially these same arguments to predict the slope of the biomass size spectrum in the oceans, although they did not use the term particle-size-conversion efficiency. The left-hand equality in equation 3, with $u = 1$, is analogous to the equation shown in fig. 3 of Sheldon et al. (1977), except that they described body size on the basis of equivalent spherical diameter, rather than weight. They indicated that for the known range of values for n and K_1, the ratio of B_{i-1}/B_i would not be too far from unity. This is analogous to saying that ϵ is approximately equal to n (equation 4). Using their value of n, this gives $n = \epsilon = 0.24$ ($n = 0.72$ if body size units are diameter rather than weight).

Kerr (1974) expanded on the theoretical analysis of biomass at adjacent trophic levels. His equation 7 is equivalent to equation 3 above for $u = 1$ if the exponents of the allometric relationships between body size and growth rate, and body size and metabolism, are equal. Kerr estimated $n = 0.2$, a predator–prey size (mass) ratio of 8000, and a K_1 of 0.14 (0.7 times a net growth efficiency of 0.2). This gives $\epsilon = 0.22$, with a resultant small decrease in spectrum biomass with increasing body size (i.e. $n - \epsilon = -0.02$). By comparison, Borgmann and Whittle (1983) estimated ϵ at 0.26 from data on PCB and DDT concentrations in biota from Lake Ontario. For the same lake, Borgmann (1985) estimated n at 0.24, equivalent to the estimate of n by Sheldon et al. (1977) for marine species. This again gives a size spectrum with a gradually decreasing biomass with increasing size ($n - \epsilon = -0.02$).

Pelagic ecosystems are in reality composed of food webs. Any species may feed on more than one lower trophic level, and predator–prey size ratios are therefore variable. This makes it difficult to define the trophic level of larger organisms precisely. However, Borgmann (1982) has shown that this need not invalidate the use of equations 2 and 4, as long as ϵ remains constant. The available data do, in fact, indicate that this is not an unreasonable assumption (Borgmann 1982). Consequently, the fact that real ecosystems are composed of food webs, rather than food chains, does not seriously impair the equations discussed above.

Continuous Size Spectra

Pelagic ecosystems do not consist of food chains, or webs, in which each trophic level has a discrete body size. There is a continual gradation of body sizes, and the smallest carnivores may be smaller than the largest herbivores. Sheldon and Parsons (1967) described such a spectrum for the plankton of Saanich Inlet, British Columbia. They plotted particle concentration (ppm wet weight) against log particle diameter, from 3 to 1000 μm, with each size class having a mean body volume twice that

TABLE 1. Biomass and production equations applicable to continuous size spectra. All integrations are from $W = W_x$ to $W = W_y$.

Biomass:

(5) $B_{xy} = \int \beta(W)dW = \int b'W^c dW = b(W_y^{n-\epsilon} - W_x^{n-\epsilon})$ (if $c \neq -1$) or $b' \ln (W_y/W_x)$ (if $c = -1$)

Production:

(6) $P_{xy} = \int \beta(W)aW^{-n}dW = \int ab'W^{-\epsilon-1}dW = d(W_y^{-\epsilon} - W_x^{-\epsilon})$

Size-corrected production:

(7) $P_{xy}^* = \int \beta(W)aW^{-n}W^{\epsilon}dW = \int ab'W^{-1}dW = ab' \ln (W_y/W_x)$

Parameters used in the above equations:

$c + 1 = n - \epsilon$

$F = ab' \ln (\text{PPR})$

$\beta(W) = b'W^c = FW^{n-\epsilon-1}/(a \cdot \ln (\text{PPR}))$

$d = ab'/-\epsilon = -F/(\epsilon \cdot \ln (\text{PPR}))$

$b = b'/(n - \epsilon) = F/(a(n - \epsilon) \ln (\text{PPR}))$

Definitions:

PPR = mean predator–prey size (mass) ratio

ϵ = −log (conversion efficiency)/log (PPR)

aW^{-n} = biomass turnover rate (P/B)

F = biomass flow up the size spectrum = $P_i W_i^{\epsilon}$ or P_{xy}^* if W_y/W_x = PPR

of the next smallest size class. Additional examples are given by Sheldon et al. (1972). In an attempt to create a more realistic model of biomass flow up the food web, Platt and Denman (1977, 1978) developed a model based on such a continuous size spectrum. They first defined a normalized size spectrum, $\beta(W)$, such that the biomass over a size range (ΔW) is $\beta(W) \cdot \Delta W$. This is necessary because biomass must always be expressed relative to some size range. A plot of biomass against body size has no meaning unless the width of the size classes is carefully defined. The normalized size spectrum can be defined independent of the size range, and biomass within any size class is then simply the area under the graph of $\beta(W)$ against body size. Platt and Denman (1978) chose size classes such that $\Delta W \approx W$ (an octave, or logarithmic, scale) giving $B \approx \beta(W) \cdot W$ for a size band. Biomass flux up the size spectrum was estimated as the turnover rate within any narrow size band. The rate of decrease in this flux with increasing size was estimated as the respiration rate. Solving their equations gave a formula similar to equation 4 (equation 26 in Platt and Denman 1978), but with $n - \epsilon$ replaced with a different exponent.

Platt and Denman's model is not directly comparable with other models of the biomass size spectrum because it does not contain any explicit mechanism by which biomass can disappear from one size and reappear at a considerably larger size, such as occurs during predation (T. Platt, pers. comm.). This is why their exponent is different from $n - \epsilon$, and the resultant slope of their spectrum is much steeper than predicted by other models. It is possible, however, to introduce a term for predation into Platt and Denman's formulation by assuming that biomass flux due to predation is proportional to turnover rates. It can be shown that this results in equations analogous to Platt and Denman's, but with an additional proportionality constant. The result is a predicted slope for the biomass size spectrum equivalent to that given in equation 3.

In Platt and Denman's model, as in Sheldon's spectrum (Sheldon and Parsons 1967; Sheldon et al. 1972), the width of each size class was defined such that the maximum body size was twice the minimum size within each class. In practice, however, field data are often collected over variable size ranges (e.g. Borgmann 1985). A comparison of biomasses of different sizes of organisms would be desirable, even if the widths of the size classes vary in an arbitrary fashion. This can be done by defining a continuous biomass function (similar to Platt and Denman's normalized size spectrum) which can be integrated to give biomass over any desired size range. B_{xy} (equation 5, Table 1) is the biomass between size W_x and W_y. Assuming that $\beta(W)$ is an allometric function of W ($\beta(W) = b'W^c$), equation 5 can be integrated. Borgmann (1985) showed that the exponent of W after integration ($c + 1$) must equal $n - \epsilon$ and used equation 5 to predict biomass over the entire size spectrum in Lake Ontario from data on the biomass of zooplankton and phytoplankton. (Note the special case where $c = -1$, which represents a completely flat biomass size spectrum.)

An equation for production over any size interval (equation 6, Table 1) is analogous to equation 5 for biomass over any size interval. This is obtained by integrating the product of $\beta(W)$ and the turnover rate (aW^{-n}) and is similar to the derivation of equations 3 and 4 from 1 and 2. Equation 6 is similar to equation 2, but whereas equation 2 describes production for a given trophic level, equation 6 describes total production over a given size range. This is particularly useful if data are available for production over a size range that constitutes more or less than one trophic level. For example, total zooplankton production could include small herbivorous species plus larger omnivorous and carnivorous species. A wide size range in zooplankton would therefore include production over more than one trophic level. Total zooplankton production could not then be used to estimate P_i in equation 2, but could still be used to estimate the constant d in equation 6. This, in turn, would allow us to estimate P_{xy} over other size ranges.

It is also possible to estimate biomass flow up the food web (F in equations 2 and 4) directly for a continuous size spectrum. This is useful for comparing the discrete trophic level equations (1–4) with the continuous spectrum equations (5 and 6). In this

case, the parameter to integrate would be what Borgmann (1982) referred to as size-corrected production, production multiplied by W^{ϵ}, or the product of $\beta(W)$, aW^{-n}, and W^{ϵ} (equation 7, Table 1). In the special case where W_y/W_x is equal to the mean predator-prey size ratio (PPR), so that the size range from W_x to W_y includes exactly one trophic level, P_{xy}* is equal to F. This allows us to calculate F from b or d (equations 5 and 6) and demonstrates that $\beta(W) = FW^{n-\epsilon-1}/(a \cdot \ln(\text{PPR}))$ (Table 1). In practice, the value of $\beta(W)$ need not be calculated for routine analysis of size spectra data. It will generally suffice to estimate b or d over some size range for which B_{xy} or P_{xy} is known and then to use this to estimate B_{xy} or P_{xy} over some other size range. In some cases it may be desirable to use the value of b or d to estimate F and calculate production at some point size (P_i, equation 2). This represents the production that would occur if all biomass were consumed by a species at this size before passing on to higher trophic levels (for an example, see Leach et al. 1987).

Somatic Growth and Reproduction

Most pelagic organisms undergo a substantial amount of somatic growth during their life cycle. This results in a change in body size and trophic level which makes it difficult to clearly define biomass flow between species in a food web. Platt and Denman (1977, 1978) have tried to circumvent this problem by using a continuous model, but as indicated above, the absence of a mechanism which accounts for predation creates a size spectrum which is unrealistically steep. Two different, but complementary, approaches have since been used to deal with somatic growth, one by Silvert and Platt (1978, 1980) and another by Borgmann (1983).

Silvert and Platt (1980) derived a general, nonlinear, time-dependent description of energy flow up the size spectrum. This model includes both somatic growth and predation. When applied to steady-state conditions, and using the assumptions that somatic growth is an allometric function of body size and that reproduction can be ignored, this model suggests that $\beta(W)$ is proportional to W^{n-k} (see also Peterson and Wroblewski 1984, who use x in place of n and c in place of k). In this solution of the model, therefore, ϵ is replaced with $k-1$, where k is equal to the ratio of the size-specific mortality rate to the size-specific growth rate and must satisfy the condition (Silvert and Platt 1980)

$$kK_1 = (\text{PPR})^{1-k}$$

where PPR is the predator–prey size ratio and K_1 is the biomass conversion efficiency. The ratio of production at two adjacent trophic levels is therefore given by

$$(8) \quad \frac{P_j}{P_i} = kK_1 = \left(\frac{W_j}{W_i}\right)^{-(k-1)}.$$

For a predator–prey size ratio of 2900:1 and a conversion efficiency of 14%, k is equal to 1.22 (Peterson and Wroblewski 1984) giving $k - 1 = 0.22$. For the same predator-prey size ratio and conversion efficiency, $\epsilon = 0.247$. Rearranging equation 8 gives

$$k - 1 = \frac{-\log(K_1)}{\log(W_j/W_i)} - \frac{\ln(k)}{\ln(W_j/W_i)}.$$

The left-hand term is equivalent to ϵ. The right-hand term is written in terms of natural logarithms to make use of the approximation $\ln(1+x) \approx x$ for small x (i.e. $x = k - 1$). This leads to

$$(9) \quad \epsilon \approx (k-1)\,(1 + 1/\ln(W_j/W_i)).$$

For predator–prey size ratios around 3000 ($\approx$14 on an equivalent spherical diameter basis (Sheldon et al. 1977, their fig. 2)), ϵ is greater than $k-1$ by a factor of approximately 1.125. The result is a slightly higher predicted biomass at large sizes relative to smaller sizes as compared with equation 4 or 5, and also a slightly higher production rate. Silvert and Platt's (1980) approach therefore predicts a slight increase in efficiency of biomass transfer up the size spectrum as a result of somatic growth. However, this slope does not take into account the effect of reproduction, which decreases the efficiency of biomass transfer up the size spectrum.

Borgmann (1983) used a different approach to estimate the effects of both somatic growth and reproduction on the efficiency of biomass flow up the size spectrum. Unlike Silvert and Platt's (1978, 1980) model, this approach does not define the effect of any specific growth or mortality rate function on the slope of the biomass size spectrum. Rather, it allows the effect to be calculated from field data on size and biomass of age classes of a species. Borgmann (1983) gave an example of how this can be done using size frequency data for *Mysis relicta* in Lakes Ontario and Superior. However, his equations can be solved and simplified for at least two specific cases. The first occurs if, during the development of a cohort, the mortality rate is matched by the growth rate, such that total biomass does not change appreciably. Then the effects of somatic growth and reproduction cancel one another, and biomass flow up the food web is still given accurately by equations such as equation 2. If it is assumed that cohort biomass remains constant when modelling the flow of biomass up the size spectrum, then somatic growth and reproduction can be ignored (Borgmann 1983).

A second condition also leads to simplification of Borgmann's (1983) equations. If we ignore reproduction and assume that the growth rate is given by aW^{-n}, and if we ignore mortality of the largest size class (B_{2f}, equation 14 in Borgmann 1983) and assume that the mortality rate is proportional to the growth rate ($dN/Ndt = mW^{-n}$), then the ratio of production at two subsequent trophic levels can be shown to be equal to $(m/a) \cdot K_1$ instead of K_1. However, m/a is equal to k in Silvert and Platt's (1980) model (equation 8), indicating that both their model and Borgmann's (1983) approach give equivalent results if the same underlying assumptions are used.

In summary, the effect of somatic growth and reproduction on biomass flow up the size spectrum can be calculated for any species whenever size frequency data are available (Borgmann 1983). In the absence of such data, the prediction of the slope of, and biomass flow up, the size spectrum requires some simplifying assumptions. One possible assumption is that cohort biomass remains constant. In this case somatic growth and reproduction effects cancel, and the biomass size spectrum is adequately described by equations 1–7. Alternatively, it may be assumed that somatic growth is an allometric function of body size and that reproduction effects are negligible. This requires that ϵ be replaced with $k-1$. Equation 9 gives an approximate conversion between ϵ and $k-1$ if the average predator–prey size ratio is known. Equation 9 indicates that, for realistic values of the predator–prey size ratio, the difference between ϵ and $k-1$ is not large. It will therefore not make much difference which assumptions are used to predict the slope of the biomass size spectrum, especially when uncertainties in the other parameters

(predator–prey size ratios, conversion efficiencies, exponents of the allometric relationships, etc.) are considered.

Discussion

The slope of the biomass size spectrum, and biomass flow (production) up the food web, can be described as a simple food chain model using simple equations (e.g. equations 1–4). In practice, the biomass size spectrum cannot always be divided into easily recognizable trophic levels, and biomass and production are often best described over a defined size range (e.g. equations 5 and 6) when dealing with real data. Although aquatic ecosystems consist of food webs, rather than food chains, this does not affect the estimate of biomass flow up the size spectrum as long as it is reasonable to assume that particle-size-conversion efficiency is constant (e.g. Borgmann 1982). Any one organism may undergo considerable somatic growth during its life cycle, and may therefore occupy several different trophic levels at different times. When mature, the organism will reproduce, resulting in movement of biomass down the size spectrum. The effect of these processes on the efficiency of biomass movement up the food web can be calculated, although the mathematics become more complicated. The processes of somatic growth and reproduction do not, however, necessarily greatly alter the slope of the size spectrum, or production within that spectrum, compared with what would be predicted for a simple food chain. For example, if growth balances mortality, then cohort biomass is constant and the simple models remain valid. Allometric relationships between growth and mortality rates and body size combined with negligible reproductive effects would improve food web efficiency slightly (i.e. replacing ϵ with $k - 1$).

The above models are all based on the general allometric relationships between body size and physiological processes, especially growth or turnover rates. These relationships are quite predictable over a large range of body size, but within any narrow size range there may be considerable variability. Real size spectra will therefore not necessarily be as smooth as predicted from equations such as equation 5. For example, an abundance of predators on zooplankton may result in low zooplankton biomass and high phytoplankton biomass. An absence of such predators will result in higher zooplankton biomass and lower phytoplankton biomass. A food chain may therefore have a sawtooth size spectrum, with every second trophic level being high and the others low. Manipulation at the top of the food chain may invert this pattern. Biomass flow through the size spectrum will still decrease more or less uniformly with body size (e.g. equations 1 and 2), but each second trophic level may be near its maximum turnover rate and the others near their minimum turnover rate. The overall slope of the biomass size spectrum cannot therefore be reliably extrapolated from only biomass data for two adjacent trophic levels. Either data are needed for at least three trophic levels, or independent estimates of n and ϵ (or k) are required. Equation 5 should still provide reasonable estimates of biomass under such conditions if biomass is integrated over a size range sufficient to include two trophic levels in each size class.

There are a few other restrictions to the application of the above models. Biomass must, of course, taper off at some maximum and minimum size, and production of the smallest and largest size classes may not fit the model. The largest size class, unless harvested commercially, will not have any predators and will therefore have no net production, other than what is required to offset natural mortality. It is also assumed that there are no natural bottlenecks in the food web. If such a bottleneck occurs, production at lower trophic levels will lead to natural mortality instead of consumption and production at larger sizes. If a relatively constant fraction of the prey production is lost through pathways other than predation at all trophic levels, then the above equations could still be applied, but ϵ would be replaced with an analogous parameter ($-\log(K_1 \cdot$ fraction of prey eaten$)/\log(W_j/W_i)$). The models also do not account for the detailed or fine structure of the size spectrum. Within a trophic level there may be a single peak of biomass or a wide flat spectrum. Which one occurs depends on the details of the biology of those species comprising each size range. Description of such fine scale features is likely to require other, species-specific models. The models described above provide primarily an overview of the slope and production of the overall size spectrum, which may help place the detailed data in perspective and provide clues as to what might be needed in more detailed models.

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Understanding Recruitment of Lake Michigan Fishes: The Importance of Size-Based Interactions Between Fish and Zooplankton

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Mechanisms controlling recruitment of fishes appear to be strongly size dependent. It is now established that size-selective predators can dramatically reduce zooplankton size, but little is known about the effects of zooplankton size on growth and recruitment of fish through the post-larval stage. As fish grow, their optimal prey size increases; if large zooplankton are uncommon, growth rates may be reduced, prolonging vulnerability to predation or other size-dependent mortality sources and thus reducing recruitment. Most Lake Michigan fishes, including offshore species such as bloater (*Coregonus hoyi*) and nearshore species such as yellow perch (*Perca flavescens*), shift from feeding on zooplankton in their early years to feeding on benthic prey or to piscivory. Predation mortality on many larval and juvenile fishes including bloater and yellow perch has been shown to be size or growth rate dependent. As alewife (*Alosa pseudoharengus*) increased in abundance in Lake Michigan in the 1960s, large zooplankton declined and both bloater and perch recruitment was poor. In the late 1970s and early 1980s, alewife declined, large zooplankton increased, and strong year classes of bloater and perch were formed. Based on these dynamics and recent research on resource use, foraging behavior, and recruitment dynamics of larval and juvenile fishes, we suggest two hypotheses. First, young-of-year and juvenile pelagic fishes may have the major size-structuring effects on epilimnial zooplankton in Lake Michigan. And second, if large zooplankton are uncommon, as they were in Lake Michigan in the 1960s, growth rates and recruitment of native fishes will be reduced. Size-based interactions between fish and zooplankton appear to have important implications for growth and recruitment success of fishes.

Les mécanismes régissant le recrutement des poissons sont fortement dépendants de la taille. Il est maintenant établi que les prédateurs sélectifs quant à la taille peuvent réduire de façon extrême la taille des organismes zooplanctoniques mais l'on connaît peu de choses des effets de la taille de ces organismes sur la croissance et le recrutement des poissons au cours de l'étape post-larvaire. À mesure que les poissons grandissent, la taille de leurs proies optimales augmente aussi; leur taux de croissance peut être réduit si les gros organismes zooplanctoniques sont rares, ce qui prolonge le période de vulnérabilité à la prédation ou à d'autres causes de mortalité fonction de la taille et réduit ainsi le recrutement. La plupart des poissons du lac Michigan, y compris les espèces du large, comme le cisco de fumage (*Coregonus hoyi*), et celles se rencontrant près des rives, comme la perchaude (*Perca flavescens*), se nourrissent de zooplancton au cours de leurs premières années et se nourrissent ensuite de proies benthiques ou deviennent piscivores. Il a été montré que la mortalité par prédation des larves et des juvéniles de poisson, dont le cisco de fumage et la perchaude, était fonction de la taille ou du taux de croissance. L'augementation de l'abondance du gaspareau (*Alosa pseudoharengus*) dans le lac Michigan au cours des années 1960 s'est traduite par un déclin des gros organismes zooplanctoniques, et le recrutement du cisco de fumage et de la perchaude a été faible. Vers la fin des années 1970 et au début des années 1980, le gaspareau est devenu moins abondant et l'on a noté une augumentation des gros organismes zooplanctoniques et l'apparition de fortes classes annuelles chez le cisco de fumage et la perchaude. En se basant sur cette dynamique et les résultats de recherches récentes sur l'utilisation des ressources, le comportement de recherche de nourriture et la dynamique du recrutement des larves et des juvéniles chez les poissons, les auteurs proposent deux hypothèses. Selon la première, les poissons nés au cours de l'année et les juvéniles pélagiques pourraient être les organismes qui ont le plus important effet sur la structuration des tailles du zooplancton de l'épilimnion dans le lac Michigan. Selon la seconde, lorsque les gros organismes zooplanctoniques sont rares, comme cela était le cas dans le lac Michigan au cours des années 1960, il y a réduction du taux de

croissance et du recrutement des poissons indigènes. Les interactions entre la taille des poissons et celle des organismes zooplanctoniques ont des effets importants sur la croissance et le succès du recrutement des poissons.

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The predator–prey relationship between fishes and zooplankton populations is a strong, two-way interaction; each component has major, direct effects on the other, with substantial indirect effects extending to other trophic levels. Zooplankton communities can be shaped by size-selective predation by vertebrates (Hrbacek 1962; Brooks and Dodson 1965; Galbraith 1967; Wells 1970; Hall et al. 1976; Lynch 1979; O'Brien 1979; Zaret 1980) as well as by invertebrate predation (Dodson 1974; Zaret 1975; Kerfoot 1977). If fish are absent, large invertebrate predators and herbivores tend to predominate; if fish are present, invertebrate predators and large herbivores are reduced because fish take larger than average sized zooplankton. Shifts in size structure of the zooplankton community can, of course, lead to shifts in the phytoplankton community (Gamble 1978; Lynch and Shapiro 1981; Steele and Gamble 1982) and influence lake trophic state (Lynch and Shapiro 1981; Kerfoot 1983; Carpenter and Kitchell 1984).

Fish interactions with the plankton community have strong ontogenetic components. Most fishes first feed in the plankton, either on small phytoplankton or on nauplii or copepodite zooplankton. As they grow, they typically shift to progressively larger zooplankton, eventually becoming size selective on large herbivores and invertebrate predators; larger juvenile or adult fish often shift to different habitats or diets. Thus, fishes that play quite different ecological roles as adults (herbivore, benthivore, piscivore) may all feed upon plankton as larvae and juveniles.

Although fishes routinely shift up in prey size preference with increasing fish size (Hunter 1981), and optimal diets include progressively larger prey (Werner 1974, 1977), little experimental evidence exists to test the idea that fish grow faster on optimally sized prey (Paloheimo and Dickie 1966; Wankowski and Thorpe 1979). Abundant data support the idea that larval and juvenile fishes grow more slowly if food density is reduced, but few data exist to address the effects of zooplankton size per se. If zooplankton size structure is shifted to small sizes due to intense size-selective planktivory, do growth rates of juvenile fishes decline?

Understanding the mechanisms governing recruitment success and ultimately year class formation of fishes is a key problem in fisheries research (Steele et al. 1980; Rothschild and Rooth 1982). Mechanisms likely to influence survival and recruitment are largely size dependent. While the early life history represents only a brief portion of the life span, the most dramatic changes in size occur during this time. A typical fish which may increase five orders of magnitude in weight over its entire life span may grow three orders of magnitude within the first few months. As size increases, larvae and juveniles may encounter a series of "bottlenecks" due to predation by or competition with juveniles or adults of other species, or even adults of their own species (MacCall 1981; Werner and Gilliam 1984). The concept of recruitment bottlenecks and ontogenetic shifts supports the idea that year class strength is determined not just at first feeding or even in the larval stage, but that there may be a series of hurdles to be met and that these may extend through at least the first year of life (Sharp 1981; Rothschild and Rooth 1982).

Events early in the ontogeny of fishes play a large part in determining population dynamics of the adults. Thus, the interaction between the zooplankton community and larval and juvenile fishes may represent a pivotal focus for total system dynamics and fish community structure. In this paper, we examine evidence for the importance of this interaction and explore its implications in the context of the Lake Michigan system

The Lake Michigan System

A number of characteristics of Lake Michigan make it useful for examining fish-zooplankton interactions and recruitment processes in fishes. First, the extent of historical manipulations of the planktivore–zooplankton system and their documentation are perhaps unparalleled. Second, Lake Michigan, while moderately large (1/10 the area of the North Sea), is a relatively closed system. Third, Lake Michigan is a low diversity system relative to many nearshore marine systems. Potential vertebrate predators on larvae or juveniles of a particular fish species can be limited to just a few species; potential invertebrate predators on larval or juvenile fishes are limited one mysid shrimp and two or three species of copepods. These last two characteristics suggest that the Lake Michigan fish community may be more poorly buffered and less resilient to change than nearshore marine fish communities. However, due to the relative simplicity of the system, many of the potential interactions can be explored experimentally in the laboratory or in the field.

The major planktivore species in the offshore pelagic zone are the alewife (*Alosa pseudoharengus*), bloater (*Coregonus hoyi*), and rainbow smelt (*Osmerus mordax*), and the nearshore zone is dominated by alewife and yellow perch (*Perca flavescens*). Although our understanding is incomplete for many cells of the Lake Michigan "species interaction matrix," recent laboratory and field observations on resource use, foraging behavior, and recruitment dynamics of larval and juvenile fishes provide clues for interpreting both the historical and contemporary data.

Alewife – Native Species Interactions and Zooplankton Size

Available data on the feeding behavior of adult and juvenile alewife suggest that the alewife is much more efficient than native species at feeding on small zooplankton, based on its ability to switch feeding modes from particulate feeding to filtering (Janssen 1976; Crowder and Binkowski 1983; Crowder 1985a). When alewives reached their peak abundance in 1966, zooplankton larger than 1 mm body size were rare in the plankton (Wells 1970), presumably due to alewife feeding. Correlated with the alewife increase and decline in zooplankton size were declines in bloater, yellow perch, and several other

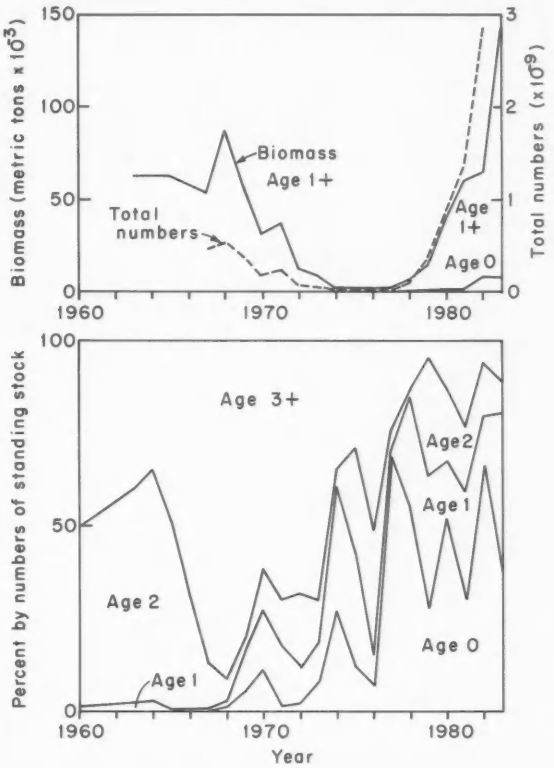

FIG. 1. Bloater numbers and biomass available to USFWS bottom trawls (October 1960–83) based on data from E. H. Brown, Great Lakes Fishery Laboratory, USFWS. Top panel shows total numbers of bloater standing stock (broken line) and estimated biomass of age 0 and age 1+ bloaters (solid lines). Bottom panel shows percentage of standing stock available to trawls by age group.

native species. Recruitment failure has been suggested as the cause for the rapid decline and shift in population age structure of bloater (Brown 1970) and yellow perch (Wells 1977) in the late 1960s and early 1970s. The commercial catch of yellow perch decreased substantially in the mid-1960s (Wells 1977), and a few years later, bloater catches began to decline such that the commerical fishery for them was closed lake wide by 1976 (Brown et al. 1985).

Among the native species, the interaction of bloater with alewife is best understood. When zooplankton are small, as they were in 1966, foraging costs for young-of-year bloater increase dramatically (Crowder and Binkowski 1983). But adult bloater appear to be more efficient than adult alewife when foraging on benthic prey (Crowder and Binkowski 1983). The zooplankton feeding stage in juvenile bloater thus becomes a potential bottleneck (sensu Werner and Gilliam 1984) for recruitment of larger bloaters to the benthos. If bloaters make it through the zooplankton feeding stage, they should succeed in the benthic habitat relative to alewife. If the bloater decline in the late 1960s was due to competition for zooplankton with alewife, we might expect to find evidence of niche shifts or morphological shifts in response to this competition.

Crowder (1984) found that bloaters collected from southeastern Lake Michigan in 1979 had significantly fewer (by 2.1) and significantly shorter (by 15%) gill rakers than bloaters collected there in 1960. The mechanism underlying this shift in raker morphology is difficult to document unequivocally, but competition with alewife may have contributed to this change. Our data also suggest that in the late 1970s juvenile bloaters in late summer shifted to the bottom habitat and benthic prey as much as 2 yr earlier than bloaters caught in the late 1950s before alewife became abundant (Crowder and Crawford 1984). Before the alewife population increase in Lake Michigan, only bloaters greater than 230 mm fork length (FL) (about age 5 or more) ate greater than 99% benthic prey; now, yearling fish about half as long do so (Crowder and Crawford 1984). This earlier ontogenetic shift to the bottom habitat is not a recent phenomenon, but apparently began in the late 1960s (Fig. 1; E. H. Brown, Great Lakes Fishery Laboratory, unpubl. data). Age 0 bloaters first appeared in bottom trawls in 1968. These and yearling bloaters accounted for less than 10% of October bottom trawl catches until 1969. In the late 1970s, however, age 0 and 1 bloaters accounted for 60–80% of the bottom trawl catch (Fig. 1) although total numbers of bloater caught did not differ from the late 1960s.

For yellow perch, the mechanisms causing poor recruitment when alewives were abundant are unknown, but reduction in the appropriate size food particles for young-of-year yellow perch cannot be ruled out (Wells 1977). Mills et al. (1984) showed in the field and in laboratory experiments that at 25–30 mm, age 0 Oneida Lake yellow perch switched from copepods to larger daphnids, especially *Daphnia pulex*. Mean prey size increased linearly as fish size increased from 18 to 59 mm, and although 30–60 mm perch did not select the very largest prey available, mean prey sizes selected ranged from about 1.2 to 1.8 mm. These sizes of zooplankton were rare in Lake Michigan when alewife were abundant in the mid-1960s. Growth rates of young-of-year yellow perch in Oneida Lake were greatest when *D. pulex*, a relatively large daphnid, was available (Mills and Forney 1981). Nielsen (1980) has shown that accelerated first year growth of Oneida Lake perch translates into a reduced period of vulnerability to predation by walleyes (*Stizostedion vitreum vitreum*) and results in higher recruitment. It seems likely, then, that reduced zooplankton size when alewives were abundant in Lake Michigan reduced growth rates and thus recruitment success of yellow perch.

Taken together, the evidence cited above supports the idea that as alewife increased, zooplankton size was severely reduced, and that led to poor recruitment in native species. Based on laboratory behaviors, we expect that juvenile bloaters were inefficient foragers on the small zooplankton which were common in the mid-1960s. The bottleneck due to the reduction of large zooplankton appears to have been severe enough to generate both ecological and morphological shifts in bloater relative to the period before alewife became abundant. Zooplankton size structure also creates a potential bottleneck for yellow perch recruitment mediated by size-dependent predation.

Recruitment and Larval Ecology of Lake Michigan Fishes

Until recently the mechanisms governing survival and recruitment of the major Lake Michigan fishes have not been studied in detail. Over the past few years we have used a combination of laboratory experiments, field sampling, and otolith analysis to address this question for the bloater. In laboratory experiments, we examined bloater susceptibility to starvation and predation and the potential interactions between

these factors (Rice et al. 1987a). Newly hatched bloater larvae are fairly large (9.5–10.0 mm total length (TL)) and were extremely resistant to direct starvation; 50% of starved bloater larvae survived 25 d after hatching, and some individuals survived 35–40 d at near-ambient Lake Michigan temperatures. Bloaters did not exhibit a "point of no return" (irreversible starvation); fish fed later simply began growing at rates similar to those of fish fed earlier. Bloater larvae were strong swimmers, swimming about 50% of the time within 1 h after hatching and almost 100% of the time after 6 h. Even 21 d after hatching, starved larvae were still swimming continuously at 0.9 cm/s. Food deprivation did affect swimming speed; after 21 d, fed larvae were swimming almost five times as fast as starved larvae.

Bloater larvae were very susceptible to predation (Rice et al. 1987a). In laboratory trials, larvae up to 30 d old, whether fed or starved, were captured with about 80% success by 95 and 135 mm TL bloaters and 100 mm TL alewives. However, smaller larvae were more susceptible to predators than larger larvae, and starved larvae were more susceptible than fed larvae of a similar size. Given their resistance to starvation and their strong swimming ability, bloater larvae probably do not starve to death in nature due to low food encounter rates. But starvation or low food availability may be an indirect contributor to mortality, as reduced growth and swimming capabilities may result in increased or prolonged susceptibility to predation.

Our approach in the field was based on the premise that differences between larvae in the small fraction that survive the first few months of life and larvae sampled at earlier points in the life history can convey important information about sources of mortality. We used otolith analysis (Rice et al. 1985) to identify stress periods and to determine age, first feeding date (a close correlate of hatching date), and average growth rates of individual bloater larvae from hatching to nearly 2 mo of age in Lake Michigan in 1982 and 1983 (Rice et al. 1987b). In both years, growth rates of all larvae collected in the field were as high or higher than those reared in the laboratory on ad libitum rations. However, in 1982, larvae hatching early in the season had much lower growth rates during the first 3 wk of life than those larvae hatching later. These early hatching, slower growing larvae were also more likely to exhibit stress marks in the otolith ring pattern similar to those caused in the laboratory by short periods of starvation or low ration. In both 1982 and 1983, early hatching larvae apparently experienced higher mortality than late hatching larvae; early hatching larvae were significantly underrepresented among larvae surviving to 1–2 mo of age when compared with larvae sampled just a few days after hatching and to the expected hatching distribution predicted from observed egg deposition (Rice et al. 1987b).

The high growth rates of larvae collected in the field confirm laboratory results suggesting that direct starvation is not an important source of mortality for larval bloaters. However, indirect effects may be important; larvae hatching during the period of higher relative mortality early in the season were characterized by lower growth rates and a higher frequency of stress marks. These data suggest that size or growth rate dependent predation during the first few weeks of life may be a major mechanism affecting bloater survival and recruitment success. Results from the laboratory experiments on susceptibility of bloater larvae to predation are consistent with this hypothesis, and the limited published data suggest that potential predators of bloater larvae may be more abundant early in the season. Taken together, this suggests that observed differential recruitment over the season may have been due to differential predation pressure.

Our field data indicate that sometime during the period from spawning to about 1 mo after hatching, a dramatic reversal in year class strength occurred between 1982 and 1983; while relative egg deposition in 1983 was only 57% of that in 1982, the abundance of bloater larvae in 1983 surface samples was 2.4 times greater than in 1982 (Rice et al. 1987b). Obviously, events during this period played a major role in bloater survival and recruitment. Our 3 yr of field data on relative bloater year class strength based on collections of 1- to 2-mo-old fish appear to be correlated with bloater young-of-year assessments near our study sites by the U.S. Fish and Wildlife Service (Table 1). Although we will soon have more data, current results suggest that at least in the 1980s during a period of strong alewife decline, bloater year class strength may be determined in the first few months of life. However, during the peak abundance of alewife in the 1960s, additional factors (e.g. zooplankton size) may have influenced year class strength by reducing growth rates and prolonging vulnerability to predation.

Mechanisms governing recruitment of yellow perch in Lake Michigan may be similar to those in Oneida Lake. Growth of juvenile yellow perch in Oneida Lake is rapid (Vashro 1975) and zooplankton production is high relative to consumption by yellow perch, so direct starvation is not likely to be important (Noble 1975). Forney (1977) showed that predation accounts for most of the mortality in age 0 perch. Oneida Lake yellow perch cohorts vary 45 times in abundance at age 0, but may vary 300 times by age 3 (Clady 1976), suggesting that ultimate year class strength is strongly influenced by mortality of age 1 and 2 perch (Nielsen 1980). Predation by walleyes is probably the major source of mortality at this stage, and is likely size dependent (Nielsen 1980).

Much less is known of the recruitment and larval ecology of the other Lake Michigan planktivores. Size at hatching is much smaller for alewife (2.5–5.0 mm) and smelt (4.1–6.0 mm) than for bloater (9.5–10.0 mm), so direct starvation effects may be more important for these species; starved alewife larvae reach 100% cumulative mortality only 6–9 d after hatching (F. P. Binkowski and J. A. Rice, unpubl. data). However, resistance to starvation increases dramatically after just a few days of feeding (Hunter 1981), and these larvae should be attractive prey items for predators, so we might expect similar size-dependent predation effects to be important for these species as well.

System Responses to an Alewife Decline

The most recent major change in the Lake Michigan system has been a dramatic decline in alewife abundance. Based on bioenergetics modeling of the salmonid–alewife interaction, Stewart et al. (1981) forecast the possibility of an alewife decline due to excessive salmonid stocking. In fact, the alewife biomass decline probably began in the mid-1970s (Crowder 1985b), but did not become obvious until 1982. By fall 1984, the adult alewife biomass available to trawls declined to the lowest level since the early 1960s (Wells and Hatch 1985); bloaters exceeded alewife in abundance in 1982 (Wells 1985).

Concomitant with the alewife decline, large zooplankton have increased in abundance in Lake Michigan. In particular, size shifts have been apparent in the cladoceran community of the offshore zone (>30–55 m) in southeastern Lake Michigan (Gitter 1982). This size increase reflects declines in the

TABLE 1. Bloater year class strength estimates based upon egg deposition data (Wisconsin DNR), Neuston net surveys of 1- to 2-mo-old post-larvae, and U.S. Fish and Wildlife Service trawl surveys. USFWS survey data are shown for Waukegan (the station nearest our study area) and for the southern basin. All data are standardized to 1.0 for 1982. The period 1982–84 can be considered to be "good years" in terms of zooplankton size and abundance as well as overall bloater growth.

Year	Egg deposition	Neuston net	Waukegan	Southern basin
1982	1.0	1.0	1.0	1.0
1983	0.6	2.4	2.0	1.8
1984	0.8	2.6	2.4	1.8

abundance of *Bosmina* and increases in the abundance of larger *Daphnia retrocurva* and *D. galeata*. An even larger daphnid, *D. pulicaria*, first appeared in our samples in 1979–80 but was still rare in 1981. *Daphnia pulicaria* became extremely common by late summer 1982. Evans (1985) had similar results showing increases in large zooplankton in the offshore zone dating back to the mid-1970s and documented a dramatic increase in *D. pulicaria* in the summer of 1983, when *D. pulicaria* became the most common daphnid in the offshore zone. These shifts in zooplankton size structure led to dramatic increases in total grazing pressure by the zooplankton on the phytoplankton and increased water clarity (Scavia et al. 1986).

Bloaters, rainbow smelt, and yellow perch have experienced dramatic improvements in recruitment during the 1980s (Wells 1985). All three of these fishes shift ontogenetically from plankton feeding to benthic feeding and/or piscivory. The availability of large prey during their zooplankton feeding period could influence recruitment success. When zooplankton were small in the late 1960s, these planktivores experienced declines and poor recruitment. In the 1980s, strong recruitment coincided with abundant large zooplankton.

With the dramatic increase in bloater abundance and the fact that all age classes from yearling through adult are now on the bottom feeding on the same prey (a mysid shrimp (*Mysis relicta*) and an amphipod (*Pontoporeia hoyi*), Crowder and Crawford 1984), one might expect both a reduction in bloater growth rates on the bottom and perhaps a reduction in the densities of *Mysis* and *Pontoporeia*. Based on preliminary analysis of bloater growth rates, yearling bloaters caught on the bottom in August 1984 were growing 20–30% more slowly than bloaters caught from the same sampling site in 1979 (M. E. McDonald and L. B. Crowder, unpubl. data). Both *Mysis* and *Pontoporeia* appear to have declined in density since the late 1970s (M. E. McDonald and L. B. Crowder, unpubl. data).

Yellow perch and smelt may also be encountering new bottlenecks. Both have shown strong recruitment in the last few years. However, age 2+ yellow perch are now about 40% shorter in total length than they were in the 1970s (Wells and Hatch 1985; M. E. McDonald and L. B. Crowder, unpubl. data). The total lengths of age 1+ smelt are now also shorter by about 35% than they were in the late 1970s (M. E. McDonald and L. B. Crowder, unpubl. data). With strong recruitment, but smaller, older fishes, we suggest that a bottleneck now occurs in the juvenile rather than in the larval stage. The impacts of large numbers of these relatively small fishes on the zooplankton community and future recruitment remain to be determined.

Fish–Zooplankton Interactions and Recruitment

When the responses described above are considered in the light of available theory on fish–zooplankton interactions and the ontogenetic niche of fishes, two major hypotheses follow. First, we hypothesize that juvenile pelagic fishes rather than adults may have *the* major impact on shifts in epilimnial zooplankton size. Large adult alewives in Lake Michigan are constrained primarily to the lake bottom during the day and migrate off the bottom as far as the thermocline at night (Janssen and Brandt 1980). Thus, during the period of lake stratification, adult alewives are basically not feeding at any time of the day above the thermocline. *Daphnia* species aggregate in the upper metalimnion during the day and move upward into an epilimnion at night (Gitter 1982), and so are not likely to be influenced directly by adult alewife, at least in the offshore zone. In contrast, juvenile alewife, smelt, and young-of-year bloater are common in the epilimnion in the offshore zone of the lake (Crowder and Crawford 1984; Rice 1985; J. Magnuson and L. B. Crowder, unpubl. data). Can these juveniles be size-selective predators on the epilimnial zooplankton during thermal stratification? At what ages and sizes can they begin to have these effects?

Janssen (1976) found that in the laboratory, young-of-year alewives averaging only 57 mm TL were positively size selective on a natural mix of zooplankton sizes collected from the field. Young-of-year alewives, smelt, and bloaters (30–40 mm mean TL) which occupy the epilimnion in late August have mouth widths which would allow them to consume larger than average zooplankton in late summer and fall (A. Geffen and J. Magnuson, University of Wisconsin, unpubl. data). This is also when the cohort of young-of-year planktivores places its peak demand on zooplankton resources. Stewart (1980) modeled consumption by an alewife cohort using a bioenergetic model and concluded that 50–60% of the lifetime food consumption by alewives occurs in their first 2 yr. Seasonally, consumption peaks for both young-of-year and yearlings in late August – September. Thus, not only do juvenile alewives become large enough late in the first summer of life to become size-selective predators, but their cohort consumption peaks at that time. Based on field growth rates of larval and juvenile bloaters (Rice et al. 1987b), the average bloater in late August – September would be expected to be 45–55 mm TL, so they too could be strongly size selective. We have less information for smelt growth or prey selection, but our trawling studies in late August – September (Brandt et al. 1980; Crowder and Magnuson 1982) caught substantial numbers of pelagic young-of-year smelt (35–60 mm) which, again, could eat larger than the average zooplankton. Thus the size-selective effects of planktivory observed in Lake Michigan, as well as the indirect lower level effects that derive from them, may be due largely to young-of-year and juvenile fishes, rather than adults.

A second hypothesis suggested by the data is that if zooplankton are small (as they were in the mid-1960s), larval and young-of-year native fishes will grow more slowly than when the zooplankton includes abundant large species. As far as we know, this basic tenet of optimal foraging theory has not been tested in any planktivorous fish. The "goal" of foraging optimization is to maximize surplus power (Ware 1982), which in juvenile fish would be allocated to rapid growth. Rapid growth in the larval and juvenile stage would reduce risks of predation (Werner and Gilliam 1984), allow the fish to expand its diet to larger prey, and also allow it to attain a larger size

going into the first winter which may reduce overwintering mortality.

The idea that juvenile fish growth rates may be related to food size has only been carefully tested for one species, Atlantic salmon (*Salmo salar*) (Wankowski and Thorpe 1979). Equal volumes of one of six sizes of commercial pelleted food were offered to groups of Atlantic salmon (percent mouth width 100, 50, 25, 12.5, 6.25, and 3.125%) in 10 separate experiments using fish ranging in size from first-feeding alevins to second year smolts. They found that growth rate was closely related to food size. Maximum growth in each case was shown on only one size of particle; larger and smaller particles resulted in reduced growth.

If optimal prey size increases with body size, and if large zooplankton are rare (few greater than 1 mm body size) as they were in the 1960s, growth rates of native fishes may be reduced. Slower growth rates would likely correlate with increased predation and thus reduced recruitment, which bloaters and yellow perch experienced in the 1960s. Larger zooplankton in the 1980s should allow fast growth during the larval and juvenile stages and thus should lead to greater recruitment. Based on the data cited above which suggest that larval bloaters and yellow perch are not highly vulnerable to starvation, but that recruitment through the larval stage does appear to be growth rate or size dependent, it seem appropriate to propose the hypothesis that growth rates of bloater and yellow perch are food size dependent.

Discussion

Most of the major changes in the Lake Michigan fish community over the past half century have been precipitated by strong increases or decreases in predation pressure including lamprey-induced lake trout mortality, commercial fishing, or salmonid stocking. While many of these major perturbations originated at the top predator level, system responses were manifested at the planktivore–zooplankton interface. This paper seeks to integrate the effects of zooplankton size on recruitment of fishes with the effects of juvenile and adult fishes on the zooplankton size structure. Zooplankton size, and consequently phytoplankton species composition and population dynamics, primary productivity, nutrient cycling, and lake trophic status, are all influenced by the fish–zooplankton interaction. Young-of-year and juvenile fishes may represent a major part of the fish component in this interaction, and because recruitment is determined early in life when most fishes are planktivorous, the fish–zooplankton interaction also plays a critical role in determining the population dynamics of adult fishes.

If reduced food availability or other environmental factors lead to reduced growth rates of juveniles, and those juveniles are vulnerable to size-dependent mortality sources (e.g. gape-limited predators or overwintering mortality), overall mortality may be expected to be higher. If growth potential and mortality differ among habitats, one might expect juveniles to "trade off" potential growth in a particular habitat with its associated mortality. Werner and Gilliam (1984) have examined the ontogenetic habitat shifts of freshwater sunfishes in terms of this trade-off and suggested that in the presence of substantial predation risk, habitat shifts from vegetation to open water may be delayed beyond the optimal shift point based on growth rates alone. Based on the theory of ontogenetic shifts (Werner and Gilliam 1984) and the data from marine fishes (Cushing 1975; Shepard and Cushing 1980; Hunter 1981; Rothschild and Rooth 1982), it seems that there are potentially profound linkages between growth rate and size-dependent mortality. Vulnerability to predators may depend upon growth rate in two ways: first, if food limitations weaken the juvenile fish, they may be more directly vulnerable to predators, and second, even if slowly growing fish are not directly more vulnerable, they *do* spend longer at body sizes vulnerable to gape-limited predators. Either mechanism would contribute to the correlation of poor recruitment with slow growth.

The fish–zooplankton interaction plays a pivotal role in the behavior of the Lake Michigan ecosystem. A more comprehensive understanding of this interaction should improve our ability to predict year class strength of fishes.

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Production and Biomass Size Spectra in the Bay of Quinte, A Eutrophic Ecosystem

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From the 1940s on, the Bay of Quinte was subjected to increased point-source phosphorus loading. This and other stresses (exploitation, fish species invasion, and perhaps climate fluctuation) altered the productivity of the ecosystem and community structure. In the late 1970s, point-source loading was greatly reduced. At the same time, walleye (*Stizostedion vitreum vitreum*) produced the largest year class ever recorded and surged to abundance greater than those seen in the 1950s before its collapse. Also, the dominant invader white perch (*Morone americana*), which had flourished in the 1960s and 1970s, was almost eliminated by a low-temperature kill. Studies of the bay ecosystem before and after these events indicated that while nutrients and algae responded to changes in nutrient loadings, changes in secondary producers hinged on the changes in the fish community. Use of Borgmann's biomass size spectrum model provides a focus for the interpretation of nutrient- and predator-related changes in biomass distribution. Deviations of the biomass spectrum are interpreted. The biomass and production spectra are linked to both phosphorus concentrations, observed and predicted, and to fishery exploitation rates. The results suggest that while nutrients control the overall biomass of the ecosystem and the slope of the biomass spectrum, trophic interactions and perturbations (e.g. exploitation) determine the degree to which a smooth biomass spectrum is achieved.

À partir des années 1940, la baie de Quinte a fait l'objet de rejets ponctuels de phosphore de plus en plus importants. Ce phénomène et d'autres contraintes (exploitation, invasion par certaines espèces de poisson et, peut-être, une fluctuation climatique) ont modifié la productivité de l'écosystème de même que la structure des communautés. Vers la fin des années 1970, les rejets ponctuels ont été réduits de façon importante. Au même moment, on a noté la classe annuelle de doré jaune (*Stizostedion vitreum vitreum*) la plus importante jamais enregistrée, et le niveau d'abondance de cette espèce a dépassé ceux notés au cours des années 1950, avant son effondrement. De plus, le bar-perche (*Morone americana*), une espèce étrangère dominante qui s'était fortement développée au cours des années 1960 et 1970, a été presque éliminé suite à une hécatombe due aux faibles températures. Des études de l'écosystème de la baie, réalisées avant et après ces événements, ont montré que les matières nutritives et les algues réagissaient aux variations des rejets de maitères nutritives mais que les modifications notées chez les producteurs secondaires étaient surtout fonction de celles des poissons. L'utilisation du modèle de distribution de la biomasse de Borgmann a permis d'interpréter les modifications de la répartition de la biomasse liées aux matières nutritives et aux prédateurs. Les auteurs interprètent les écarts de la gamme de distribution de la biomasse. Les gammes de biomasse et de production sont liées aux concentrations de phosphore, observées et prévues, ainsi qu'aux taux d'exploitation par la pêche. Les résultats obtenus portent à croire

que les maitères nutritives régissent la biomasse générale de l'écosystème et la pente de la distribution de la biomasse, mais que les interactions et les perturbations trophiques (p. ex., l'exploitation) déterminent la mesure dans laquelle la courbe de distribution de la biomasse est plus ou moins lisse.

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Since Sheldon et al. (1972) presented the hypothesis that, in the ocean, there were roughly equal biomasses at all particle size ranges from bacteria to whales, there has been a development of models to explain the observation, and a growing body of evidence giving general support to the idea. Borgmann (1987) has shown that most of the models are basically the same and that biomass and production size spectra should be predictable from a consideration of mass transfers between prey and predators. Sprules et al. (1983) and Sprules and Munawar (1986) have shown that freshwater plankton biomass spectra can be interpreted in a trophic context. Several studies (Dillon and Rigler 1974; Hanson and Peters 1984; Hanson and Leggett 1982) have shown that there are strong relationships between the abundances of algae, zooplankton, benthos, and fish and phosphorus (P) concentrations in lakes. Vollenweider (1975) and others have developed the framework for predicting lake P concentrations from loadings, flushing rates, and lake morphometry. If plankton biomass can be predicted from nutrient status, fish biomass and production ought to be predictable. However, this chain of links gives no account of the dynamics of species and trophic interactions.

Kerr (1977) proposed a model of the combined effects of nutrient loading and fishery dynamics on the behavior of a lake ecosystem as expressed in a biomass size spectrum. Eutrophication raises biomass levels at the low end of the spectrum, while fishing tends to lower the biomass at the high end. Then the changes at one end of the spectrum have impacts along the spectrum, diminishing away from the initial point of change. McQueen et al. (1986) have elaborated the concepts of producer-controlled (bottom-up) and consumer-controlled (top-down) forces shaping trophic and size structure. Earlier, Shapiro et al. (1975) and others suggested that changes at higher trophic levels can cause changes at lower trophic levels.

Long-term studies (Minns et al. 1986a) of the Bay of Quinte, Lake Ontario, provide an excellent opportunity to examine and assess the usefulness of the size spectrum concept and the relative influences of bottom-up/top-down forces. The bay is a eutrophic ecosystem with a large fishery. A multiagency group has studied many aspects of the ecosystem before and after point-source P loading was sharply reduced in 1978. Coincident with but apparently unrelated to that event, substantial changes occurred in the fish assemblage.

The main objective of this study is to apply Borgmann's (1982, 1985) formulation of the biomass and production size spectrum model to data collected in the Bay of Quinte. This gives us the means of (i) partially assessing the role of bottom-up/top-down forces and (ii) predicting possible future states of the bay ecosystem.

Background

The Bay of Quinte ($A_0 = 257.4$ km^2, $\bar{z} = 9.7$ m) runs into the eastern outlet basin of Lake Ontario. The bay consists of three parts. The upper bay is shallow ($A_0 = 136.4$, $\bar{z} = 3.5$) and dominated by a large expanse of water known as Big Bay. The middle bay is a small connecting area of intermediate depth ($A_0 = 49.2$, $\bar{z} = 5.2$). The lower bay is fjord-like ($A_0 = 71.8$, $\bar{z} = 24.4$) with a long deep basin, Adolphus Reach. Hydrodynamically the bay consists of two parts, upper and middle–lower (Minns et al. 1986b). The middle-lower bay undergoes considerable exchange with Lake Ontario (Freeman and Prinsenberg 1986).

The bay has undergone considerable eutrophication, largely due to point-source P inputs (McCombie 1967; Johnson and Owen 1971; Minns 1986a). Hurley and Christie (1977) described the depreciation of the fish community and fishery. In 1972, a joint agency project (Department of Fisheries and Oceans, Ontario Ministry of Environment, and Ontario Ministry of Natural Resources) was set up to assess the bay's ecosystem response to point-source P controls planned under the 1972 Great Lakes Water Quality Agreement.

From about 1940 on, the combined effects of urban population growth, the use of sewers for waste disposal, and the increasing use of phosphate detergents caused the development of highly eutrophic conditions in the upper bay, especially in the summertime when river flows were low (Minns 1986a). These effects peaked in the mid-1960's. By this time, extensive submerged macrophyte beds had receded and important fish stocks, walleye (*Stizostedion vitreum vitreum*) and whitefish (*Coregonus artedii*), had collapsed possibly due to a variety of causes (Hurley and Christie 1977). The 1960's also saw the invasion and expansion of white perch (*Morone americana*).

In the 1970's, bans on phosphate detergents began and existing sewage treatment facilities were upgraded. In the spring of 1978, new sewage treatment plants began to operate in the Bay of Quinte's urban centres and point-source P inputs were reduced by 70%, but internal P loading was important in the bay and has retarded the response to external loading controls (Minns et al. 1986b). Robinson (1986) showed that summertime total P levels declined after point-source control began, with the greatest reductions occurring in the upper bay. Mean phytoplankton biomass decreased 43% in the upper bay and 22–40% in the middle–lower bay (Nicholls et al. 1986). Millard and Johnson (1986) showed that primary production rates and light extinction decreased in line with changes in algal biomass.

In other components of the ecosystem (zooplankton, benthos, and fish), changes have occurred but are less clearly related to changing P loading and concentrations. Cooley et al. (1986) found little or no change in zooplankton biomass and production immediately after P controls began. However, after 1981 there was a marked increase in biomass. Johnson and McNeil (1986) reported that macrobenthic biomass in the upper bay was higher in 1977 than reported for 1967–68 and lowest in the 1982–84 period. In the lower bay, benthic biomass generally decreased after 1967–68, apart from an upswing in *Pontoporeia hoyi* after 1976 when white perch collapsed (Minns and Hurley 1986).

Christie (1973) and Hurley and Christie (1977) showed how

TABLE 1. Average production (P_i), production/biomass (P_i/B_i), and sizes (W_i) at different trophic levels in the Bay of Quinte.

Trophic level	W_i range (g dry wt)	W_i (g dry wt)[a]	P_i (g dry wt·m^{-2}·yr^{-1})[f]	P_i/B_i
Phytoplankton[b]	10^{-12}–10^{-7}	10^{-10}	923.22	111.55
Zooplankton[c]	10^{-7}–10^{-5}	1.5×10^{-6}	45.38	13.83
Macrobenthos[d]	10^{-5}–10^{-3}	2.5×10^{-3}	23.35	8.05
Large fish[e]	10^{0}–10^{3}	5	2.75	1.68
Small fish	10^{-3}–10^{0}	1.0×10^{-2}	—	—

[a]Largely based on Borgmann (1985).
[b]Phytoplankton biomass (Nicholls et al. 1986).
[c]Cooley et al. (1986).
[d]Johnson and Brinkhurst (1971b).
[e]Based on average biomass and the P/B calculated for white perch (Minns and Hurley 1986).
[f]Algae dry wt = 0.186 wet wt, AFDW = 0.708 dry wt (algal carbon equals 0.50 AFDW); invertebrates dry wt = 0.150 wet wt, AFDW = 0.773 dry wt; fish dry wt = 0.294 wet wt, AFDW = 0.960 dry wt; after Cummins and Wuycheck (1971, p. 10–13) and Vollenweider (1969); long-term average values derived from data described in Minns et al. (1986a).

several fish species declined during the 1950s and 1960s. In the late 1960s and 1970s, white perch increased to a dominant position in the Bay of Quinte fish assemblage. Through this period, walleye stocks remained at low levels. In the winter of 1977–78, the white perch population suffered a major die-off attributed to unusually low water temperatures (Minns and Hurley 1986). In the spring of 1978, coincident with the start of expanded P control, the walleye population produced the strongest year class ever recorded in the bay (Hurley 1986). Since that time, white perch have not recovered to any significant degree. Overall, the trend in the fish assemblage during the 1970s and into the 1980s has been one of a decline in planktivores such as alewife (*Alosa pseudoharengus*) and an increase in piscivores, notably walleye, although somewhat aided by smallmouth bass (*Micropterus dolomieui*) (Hurley 1986).

Hurley et al. (1986) have contended that the post-P control changes in the Bay of Quinte ecosystem must be interpreted in terms of both the nutrient management and top predator changes. They argued that the white perch collapse and the resurgence of walleye had a pivotal role in altering the secondary producer system. The role of P management determined the overall biomass and productivity of the ecosystem and extended structurally only to the algae and perhaps indirectly to the macrophytes. The macrophytes have yet to show any response to P management (Crowder and Bristow 1986).

Materials and Methods

Borgmann (1982, 1985) developed a biomass size spectrum model which allows estimation of biomass and production in various size ranges. The biomass (B_{xy}) in the size range W_x–W_y ($W_y > W_x$) is given by

$$(1) \quad B_{xy} = b(W_y^{n-\epsilon} - W_x^{n-\epsilon}).$$

The coefficient n is estimated from the relation

$$(2) \quad P_i/B_i = aW_i^{-n}$$

where P_i and B_i are production and biomass and W_i is the representative size of organisms in a certain size range. The coefficient b is an integration constant and a is a constant. Borgmann (1982) called ϵ the particle size conversion efficiency which can be estimated from the relation

$$(3) \quad P_i = F/W_i^{\epsilon}$$

where F is a measure of the biomass flow up the size spectrum. Borgmann (GLFRB, pers. comm.) suggested estimating ϵ using the relation

$$(4) \quad P_{xy} = d(W_y^{-\epsilon} - W_x^{-\epsilon})$$

where P_{xy} is the production in the size range W_x–W_y, and d is an integration constant.

In this study, we used estimates of P, P/B, and W for four size ranges of biota in the Bay of Quinte (Table 1) to obtain estimates of the coefficients in Borgmann's model. Inevitably in this and similar studies, size ranges and trophic levels are used interchangeably because of the restricted size ranges sampled for each trophic grouping.

In addition, we summarized data on P content, biomass, and production for the different size range/trophic groups in the Bay of Quinte (Table 2). Altogether the size range spanned 10^{-12} to 10^{3} g dry wt divided into five intervals. We considered the bay in two parts, upper and middle–lower. The data were grouped into three different time periods: 1972–77 prior to P control and 1978–81 and 1982–86 in the post-P control period. The subdivision of the post-P control period was largely based on the changes in zooplankton biomass after 1981 and on the depression and recovery of fish biomass. The data are described in detail in Minns et al. (1986a). Extensive data were available for all but the small fish, considered to span the 10^{-3} to 10^{0} g dry wt size range.

Small fish, which include most YOY's of larger species, have not been sampled regularly. However, Leslie (GLFRB, pers. comm.) has estimated the biomass of small fish at 0.11 g dry wt·m^{-2} in the upper bay in 1981, although this is considered to be an underestimate because of low sampling gear efficiency due to clogging and avoidance of the net. Lam and Roff

TABLE 2. Patterns and trends in phosphorus, biomass, and production at different trophic levels in t

Category ($g\,dry\,wt \cdot m^{-2} \cdot yr^{-1}$)	Upper bay										
	1972–77			1978–81			1982–84				
	N	$\bar{x}$	SD	*N*	$\bar{x}$	SD	*N*	$\bar{x}$	SD	*N*	
Phosphorus ($mg \cdot m^{-2}$)	18	354.4	89.1	15	204.2	50.0	5	247.1	38.4	27	6
Phytoplankton biomass	18	11.31	2.41	11	5.44	1.99	2	7.53	0.53	27	
Gross primary production	18	1093.0	226.0	9	693.0	111.0	2	668.0	22.0	27	10
P/B	18	99.3	23.8	9	146.9	89.0	2	89.0	9.1	27	1
Zooplankton biomass	4	2.23	0.94	6	1.67	0.39	3	3.45	0.47	6	
Zooplankton production	4	46.19	11.52	6	28.90	4.65	3	65.27	11.90	6	
Zooplankton size	4	1.43	0.18	6	1.79	0.22	3	1.76	0.13	6	
P/B	4	21.83	4.31	6	17.70	2.93	3	19.20	4.39	6	
Macrobenthos[a]	4	1.46	0.59	—	—	—	3	1.22	0.68	8	
Large fish biomass[b]	18	3.75	3.20	9	0.84	0.76	2	0.90	0.31	21	
Fish Size in trawl catches	18	17.4	16.6	9	4.1	2.7	2	7.8	3.0	21	

[a]1967–77 was used for 1972–77.
[b]Based on the assumption that a trawl tow samples 0.2453 ha and that the total population to index ca

evels in the Bay of Quinte, 1972–84.

Middle–lower bay									Overall		
1972–77			1978–81			1982–84					
N	*x*	SD	*N*	*x*	SD	*N*	*x*	SD	*N*	*x*	SD
27	683.8	194.8	14	594.8	177.4	7	563.6	62.2	86	481.5	233.8
27	10.62	2.57	13	6.82	2.32	3	5.80	2.87	74	9.07	3.30
27	1017.0	125.0	14	754.0	106.0	3	710.0	8.0	73	923.0	218.0
27	100.4	23.4	13	123.6	47.2	3	142.2	60.7	72	111.6	45.1
6	3.66	0.89	9	4.77	1.42	3	8.18	1.89	31	3.83	2.12
6	40.94	11.81	9	45.64	16.34	3	65.47	26.77	31	45.38	17.52
6	1.42	0.09	9	1.51	0.13	3	1.49	0.19	31	1.56	0.21
6	11.31	2.83	9	9.62	1.85	3	7.76	1.58	31	13.83	5.64
8	6.33	3.72	—	—	—	6	2.59	0.77	21	3.60	3.18
21	2.19	1.37	13	0.76	1.27	4	1.38	0.87	67	2.06	2.34
21	6.4	3.5	13	4.4	4.8	4	8.3	7.2	67	8.8	10.5

index catch ratio for white perch was 5.61 (Minns and Hurley 1986).

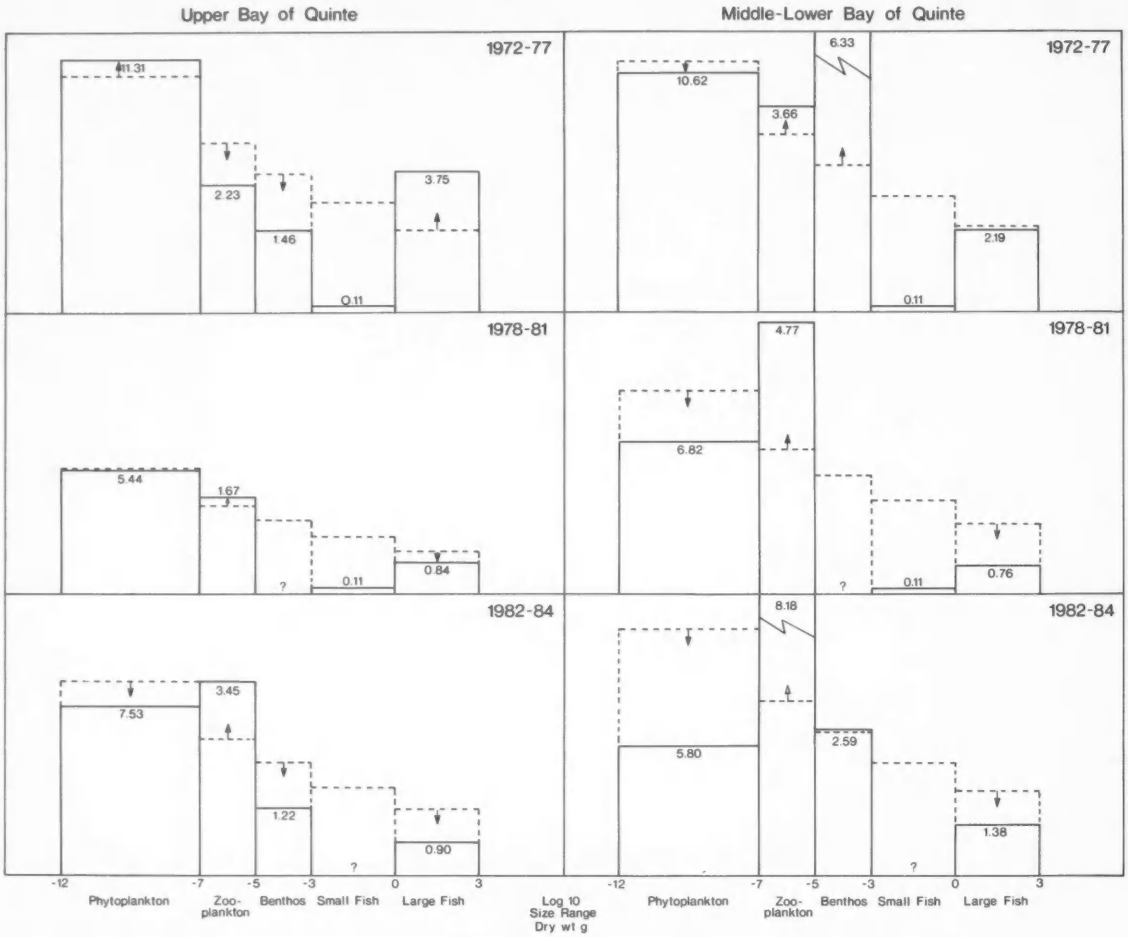

FIG. 1. Observed (—) and expected (---) biomass size spectra in the Bay of Quinte, 1972–84 (areas in boxes are proportional to biomass (g dry wt·m^{-2})).

(University of Guelph, pers. comm.) caught 134 larval fish per sample which is equivalent to 0.11 g dry wt·m^{-2}, assuming an average dry weight of 10 mg per individual. Again, the limitations of the sampling gear caused an underestimate.

Results

We compiled estimates of production (P_i), P_i/B_i, and size (W_i) for four trophic groupings (Table 1). The estimates for phytoplankton, zooplankton, and benthos were derived by conventional means. The production value for large fish was calculated using biomass estimated from trawl catches (Hurley 1986), which sample all components of the large fish assemblage, and the P/B estimated for white perch (Minns and Hurley 1986), which predominated in catches up to 1978. Based on equation (2), ln–ln regression of P_i/B_i with W_i gave an estimate for n of 0.1622 ($\ln P_i/B_i = 0.8318 - 0.1622 \ln W_i$, $N = 4$, $r = -0.986$). Values of ϵ were iteratively fit to equation (4) using the production data for the four size ranges, seeking to minimize the residual sum of squares. The estimate of ϵ was 0.2043. Therefore, the predicted value of n-ϵ was -0.042.

To allow comparison of observed and expected biomass size spectra, the sum of phytoplankton and zooplankton biomasses was used to estimate the coefficient b in equation (1) given the estimates of n and ϵ. The expected spectra for the upper and middle–lower bay areas were computed and may be compared with the measured values (Fig. 1). In all but one case (upper bay, 1972–77), phytoplankton biomass is less than expected, while zooplankton biomass is greater. Over time, observed phytoplankton biomass has tended to decrease, while zooplankton biomass increased, with the trends being greater in the middle–lower bay. Differences between observed and expected plankton biomass have become greater, with observed being less than expected for phytoplankton and vice versa for zooplankton. Benthos is less than expected in the upper bay and greater in the middle–lower. In the post-P control period, large fish biomass has been below expected levels. The estimate of small fish biomass, even if making generous allowance for underestimation, is small compared with expected levels.

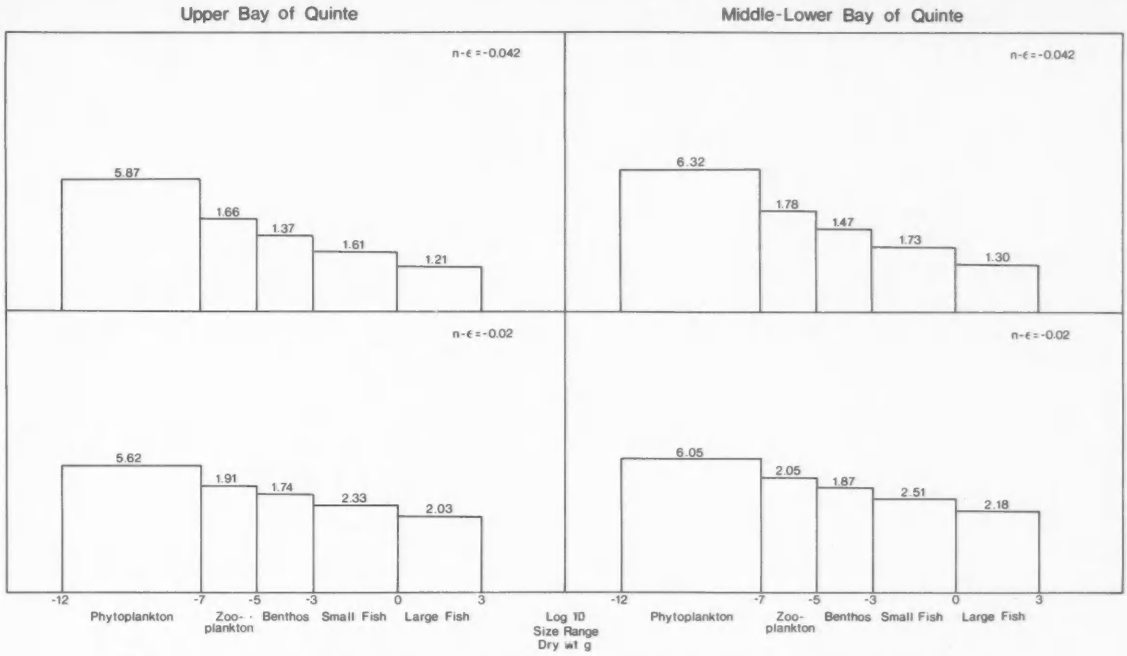

FIG. 2. Predicted biomass size spectra in the Bay of Quinte at projected phosphorus levels for two values of $n - \epsilon$.

TABLE 3. Phytoplankton plus zooplankton to phosphorus ratios and predicted steady-state phytoplankton and zooplankton biomass in the Bay of Quinte.

Category	Upper bay	Middle–lower bay
Ratio (phytoplankton + zooplankton)/phosphorus[a]		
1972–77	0.038	0.021
1978–81	0.035	0.019
1982–84	0.044	0.025
Mean	0.039	0.022
Steady-state predictions		
Phosphorus concentration ($mg \cdot m^{-3}$)[b]	44.9	21.2
Phosphorus ($mg \cdot m^{-2}$)	193.1	373.1
Phytoplankton + zooplankton	7.53	8.10

[a]Data in Table 2.
[b]Minns (1986b).

Given the means of predicting biomass size spectra from models such as Borgmann's (1982), it is possible to link biomass size spectra to assessments of the nutrient status of the ecosystem. Minns (1986b) used a P model which accounted for changes in internal loading to predict steady-state P concentrations in the Bay of Quinte. Given there is a relatively constant ratio of phytoplankton plus zooplankton biomass to P in the Bay (Table 3), steady-state phytoplankton plus zooplankton biomass can be estimated. Then as before, given an estimate of n-ϵ, the expected biomass spectrum can be calculated. We calculated the spectra for two values of n-ϵ, -0.042 and -0.02 (Fig. 2). The first n-ϵ value is the difference of the coefficients estimated here for the Bay of Quinte. The second n-ϵ value is the difference of coefficients estimated for Lake Ontario by Borgmann (1985). The steady-state condition of the Bay of Quinte might be expected to be less eutrophic than in the immediate post P control period (Minns 1986b). Thus, if the biomass size spectrum model coefficients are influenced by the degree of eutrophy, they might be expected to shift toward Lake Ontario values, Lake Ontario being mesotrophic. Sprules and Munawar (1986) have presented evidence of plankton biomass size spectra changing with P levels. The results (Fig. 2) are not appreciably different from the expected values in the post-P control period (Fig. 1), although phytoplankton and zooplankton levels would be lower.

Equation (4) can be used to calculate the production of large fish for various ecosystem states. The constant d can be estimated from the observed or expected production of phytoplankton. Assuming that the P/B of phytoplankton was a constant, and using expected phytoplankton biomasses (Fig. 1 and 2) to calculate d, we estimated expected large fish production. Then we scaled the expected production by the ratio of observed to expected large fish biomasses (Table 4).

The long-term (1956–83) average combined commercial and sports fish yield in the Bay of Quinte is 0.547 g dry $wt \cdot m^{-2} \cdot yr^{-1}$ (dry/wet ratio · wet yield/bay area or 0.294 · 479.0/257.4) (Hurley and Dentry, Glenora Fisheries Station, OMNR, unpubl. data). In the pre-P control period, large fish biomass and production were high and observed exploitation only a small proportion (10.7%) (Table 4). With the post-1977 changes in species composition from white perch to walleye dominance, large fish biomass and production have shifted to lower levels and much higher exploitation (37.7–44.5%). Application of the long-term average yield to the projected steady-state large fish biomass and production points to a moderate exploitation level (27.2%).

TABLE 4. Large fish biomass, production, and exploitation in the Bay of Quinte (g dry wt·m^{-2}·yr^{-1}).

Period	Upper bay		Middle–lower bay		Whole bay[c]			
	Biomass[a]	Production[b]	Biomass	Production	Biomass	Production	Exploitation	(%)[d]
1972–77	3.75	6.02	2.19	3.51	3.02	4.86	0.522	10.7
1978–81	0.84	1.35	0.76	1.22	0.80	1.29	0.574	44.5
1982–84	0.90	1.44	1.38	2.12	1.13	1.77	0.668	37.7
Steady state	1.21	1.93	1.30	2.08	1.26	2.01	0.547	27.2

[a]Observed (Table 3) except steady state (Fig. 2).
[b]Calculated from expected phytoplankton biomass (Fig. 1 and 2) and mean phytoplankton P/B (Table 3) and multiplied by the ratio of observed to expected fish biomass.
[c]Area-weighted sums (upper·136.4 + middle – lower·121)/257.4.
[d]Average observed exploitation for specified periods and long-term mean for the steady state.
[e]Exploitation as percentage of production.

Discussion

Borgmann's (1982, 1985) and similar models would appear to be good general descriptors of how biomass should be distributed at steady state in an aquatic ecosystem. However, it is not clear whether the biomass size spectrum should be smooth, as suggested by Lurie and Wagensberg (1983), or have peaks and troughs, as shown by Sprules and Munawar (1986) for phytoplankton and zooplankton in the Great Lakes. When dealt with in large size range sections which loosely equate to trophic levels, Borgmann's model reasonably predicts that biomass and production will decrease as one shifts up the size spectrum. Thus on a coarse scale the biomass size spectrum ought to be smooth. Meanwhile, within trophic groupings with a narrower size range, it is to be expected that both competition for similar resources, especially algae for nutrients, and size-selective consumption by their predators will result in a non-uniform distribution of biomass, as seen by Sprules and Munawar (1986).

The shaping roles of competition and predation were considered by Kerr (1977) in his concept of the biomass size spectrum. Eutrophication raises biomass levels at the low end of the size spectrum, while exploitation of fish tends to lower the biomass at the high end. In between, the web of consumers passes production up the spectrum, although stresses applied over restricted size ranges can cause "bottlenecks" in the flow. The greater than expected zooplankton biomasses in the Bay of Quinte are likely due to the imbalances further up the size spectrum. Kerr (1977) suggested that more eutrophic systems would be less efficient in passing along production. However, in the absence of severe stresses such as overexploitation, the biomass size spectrum should be smooth on a coarse scale.

The Quinte biomass size spectra showed deviations from the smooth pattern, consistent with the presence of eutrophication and exploitative stresses. Since the controls on external P loading were introduced, there has been a build-up of zooplankton. This suggests that although walleye stocks have increased substantially, there is not yet a sufficient pool of large fish (e.g. piscivores) such that the full productive potential of zooplankton can be transferred in fish biomass.

The linking of nutrients and biomass provided us with the means of predicting biomass size spectra which might be expected under different nutrient management schemes. Clearly the total biomass of an aquatic ecosystem is related to the loading and budget of nutrients, particularly P. The accumulation of P in biomass depends on the efficiency (Borgmann 1982) of the transfer of production up the size spectrum. The phytoplankton plus zooplankton to P ratios used in the Quinte calculation were derived from observations. To make the nutrient–biomass linkage more general, an independent basis for estimating the ratios would be required. As the middle–lower bay ratios were lower than those for the upper bay, the ratios were likely controlled by deep mixing in the lower bay, differences in background light extinction, and lower overall temperatures (Millard and Johnson 1986). Johnson and Brinkhurst (1971a) showed that benthic biomass and production in the Bay of Quinte was strongly determined by temperature.

Hurley and Dentry (unpubl. data) have shown that total fish yield in the Bay of Quinte has been greatest when walleye are a sustaining contributor to that yield. Prior to the recovery of the walleye and the collapse of the white perch, much of fish biomass and production was tied up in the planktivorous alewives which contribute little to the yield. May et al. (1979) presented multitrophic level exploitation models which imply that potential exploitation is greater overall when all levels are sustaining contributors to the yield. This is consistent with the concept that an ecosystem's biomass diversity must be maintained if the required level of exploitation is to be sustained (Lurie and Wagensberg 1983). The comparisons of fishery exploitation with observed and predicted biomass size spectra in Quinte appear to support the concept. Relaxation of the eutrophication stress as internal P loading dissipates should allow a smoothing of the biomass size spectrum while sustaining existing levels of exploitation. The results obtained here indicate that it should be possible to estimate the proportion of production that might be removed by exploitation without greatly perturbing the smooth flow of production up the size spectrum.

The biomass size spectrum models of Borgmann and others provide a rich basis for integrating our understanding and management of aquatic ecosystems. Clearly, both bottom-up and top-down forces are at work in determining the size and shape of biomass and production size spectra. The assessment of nutrient status, while strongly influenced by loadings, must take account of imbalances and feedback as production is passed up the size spectrum. Equally, fishery management must take account of the imbalances that can result from overexploitation or allowance of conditions that diminish the role of consumers, particularly the piscivores at the top end of the size spectrum. The Bay of Quinte has been subject to considerable changes in both its nutrient status and fish community. The results and potential benefits of these changes have not been fully realized

yet. The internal P loading has still to dissipate, thereby further reducing P concentrations, and as a result, it is expected that the macrophyte community will recover (Minns et al. 1986b). Submerged macrophytes provide essential cover for littoral piscivores such as pike and bass. Thus the restoration of habitat coupled with conservative fishery management should allow the piscivore component of the Bay of Quinte ecosystem to fully recover.

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Nonstationarity of Production Relationships in Exploited Populations

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Stock assessment usually proceeds from the assumption that there are time-invariant relationships between stock size and rate processes such as recruitment, although such relationships are difficult to discern due to noise caused by factors other than stock size. There are good biological reasons not to trust this assumption in exploited populations, where persistent environmental changes and shifts in stock structure may cause various parameters to change. Graphical and statistical procedures can be used to detect this nonstationarity in historical data sets for which stock size has varied so as to repeatedly sample a range of sizes. The policy implications of nonstationarity depend on whether the changes are clearly observable as deviations from known, long-term baseline responses. If the changes are observable, it is usually best to pretend that the current deviation will persist unless strong constraints on policy change make it necessary to plan for changes that may occur far into the future. If the changes are not observable (the usual case), then it is necessary to make a difficult policy choice between passively waiting for informative stock responses versus actively experimenting with harvest rates so as to quickly get information about responses over a range of stock sizes.

L'évaluation des stocks s'effectue habituellement en partant de l'hypothèse qu'il y a des relations invariantes dans le temps entre la taille des stocks et les processus liés à un taux comme le recrutement, bien que ces relations soient difficules à déceler en raison du bruit causé par des facteurs autres que la taille du stock. Il existe de bonnes raisons de nature biologique de ne pas se fier à cette hypothèse dans le cas de populations exploitées, où des changements environnementaux persistants et des modifications dans la structure des stocks peuvent amener la variation de divers paramètres. On peut utiliser des méthodes graphiques et statistiques pour déceler cette variation dans des série données antérieures pour lesquelles la taille du stock a varié de façon à échantillonner à plusiers reprises un éventail de tailles. Les incidences au niveau politique de la variation dépendent des changements selon qu'ils sont clairement observables comme étant des déviations de réactions de base à long terme connues, ou non. Si les changements sont observables, il est habituellement préférable de prétendre que la déviation actuelle persistera à moins que de fortes pressions sur le changement de politique ne rendent nécessaire la planification de changements qui pourraient se produire dans un avenur éloigné. Si les changements ne sont pas observables (ce qui est habituellement le cas), il est alors nécessaire de faire un choix politique difficile entre attendre passivement d'avoir des réactions des stocks qui soient informatives ou expérimenter activement des taux de capture de façon à obtenir rapidement de l'information concernant les réactions pour un éventail de tailles de stock.

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Prediction of stock responses to harvesting and other disturbances necessarily involves making assumptions about the relationship between population growth rate or surplus production and the size of the stock. Should no such relationship exist, there would be little point in harvest regulation since the stock left after harvest would not influence future harvesting opportunities. There is considerable room for debate about the best level of resolution to use in modelling the relationship (simple surplus production models versus age-structured models with recruitment, growth, and mortality versus ecosystem models that represent population rates as functions of various biophysical variables), and the relationship may be difficult to see in the face of variation caused by other factors, but most fisheries biologists would agree that it must exist at least in terms of some critical stock size below which average production rate will decline due to lack of a base for reproduction and growth.

Hidden in most of the literature on fisheries modelling and stock assessment is the assumption that there are stationary relationships between key rate processes and population size measures, provided the rates and size measures are examined in sufficient detail. By stationary, I mean a relationship that may be clouded by white (serially uncorrelated) noise but has a time-invariant statistical distribution of dependent (rate) variable values for each value of the independent (state) variable(s). This definition of nonstationarity is more restricted than is used in time series analysis (Box and Jenkins 1976, p. 7–9; Pimm and Hyman 1987) where processes with constant mean but correlated deviations are also called stationary; the restricted definition avoids possible confusion about how observers with different experience would label the same process. (Suppose productivity varies in a roughly cyclic pattern due to some environmental factor, with a "period" of 20 yr; using the standard time series definition, an observer with 10 yr of data

would likely call the system nonstationary with a trend, while an observer with 20 yr of data might call it stationary with strongly correlated residuals, and an observer with 15 yr of data would be unsure about the appropriate label.) Although any patterning of model prediction errors constitutes nonstationarity under the restricted definition, the main concern in this paper will be with persistent patterns that would be called nonstationary under the usual definition as well.

Stationarity of relationships is not expected when aggregate rates (such as total population growth rate) are predicted from aggregate state measures (such as total population size), since the composition (age structure etc.) of the state measure is expected to change systematically over time and the rate is likely to depend on this composition. It is an open question about just how detailed the model (collection of relationships) must be in order that stationary component relationships can be safely assumed, but most recipes for fisheries stock assessment and yield prediction take it as an article of faith that such a level of description does exist and can be found by diligent comparison of alternative models with data. So we blithely fit long time series of stock–recruitment data as though the older recruitment observations were still representative of what similar spawning stock sizes would produce today, plug growth curves estimated 10 yr ago into yield per recruit analyses, and pretend in the analysis of catch at age data that natural mortality rates have been constant over time.

It is unrealistic to assume stationarity in many situations, especially in the Laurentian Great Lakes where there have been major changes in the ecosystems within which the fish stocks are embedded. This paper examines some causes of nonstationarity in production relationships, reviews statistical tools for detecting nonstationarity in stock assessment data, and explores some policy consequences in terms of adaptive harvesting policies that explicitly admit nonstationarity without pretending that the changes can be anticipated far in advance.

Causes of Nonstationarity

Models for prediction of population responses consist of two types of statements or equations. First, there are accounting rules (tautologies) that define the variables and components of change to be considered, and how the components are linked. Such accounting rules will not interest us here, except insofar as they contain hidden assumptions about independence of rate processes. Second, there are functional relationships which make empirical assertions about how rates vary (or not) in response to changes in state variables such as population size. The main concern in this paper will be with the constancy of parameter values in functional relationships.

An important point to make at the outset is that the stationarity of functional relationships involving population size cannot be directly studied for natural populations simply by experimentally measuring the relationship at a series of points in time. Consider for example the "experimental production relationship" (EPR) between recruitment rate and stock size. To measure this EPR, we would need to hold the stock size constant at a series of levels while taking a large enough set of recruitment rate measurements at each of these levels to establish the mean and variability of the rate. Even if such controlled stock levels could be achieved and measurement years assigned to levels at random (i.e. move the stock up and down between levels from year to year at random), it would still take many years to establish each fix on the EPR parameters and we could not guarantee that the parameters had not changed over those years. (Errors would be random by design, yet using a nonrandom design would leave stock size and time trends effects confounded.) For stocks that are spatially structured, one might hope to measure the average EPR across substocks more efficiently by holding the substocks at a range of levels each year; however, this approach would involve making strong assumptions about similarities in parameter values among the substocks and would fail to account for (or mask) aggregate (total stock) effects that emerge from interactions (such as dispersal) among the substocks.

In the end, all we can practically measure are fragments of the EPR for different time slices as responses over narrow ranges of density during those slices. In assuming stationarity, the data analyst and model builder pretend that the same EPR is sampled in every time slice, without regard to the sequence (history) of experimental conditions (stock sizes) sampled in previous slices. Even physical scientists are leery of such sequential experimental designs, if for no other reason than a concern over instrument drift (changes in monitoring procedure parameters) between slices. Biologists should be even more concerned for the same reason and also because (1) the experimental environment cannot be fully controlled over time and (2) many factors, at all levels of biological organization, may vary with the particular history that the system has experienced. For the remainder of this section, I will ignore the monitoring change problem (see Shuter et al. 1987) and elaborate further on nonstationarity due to environment and history.

Systematic Changes in the Ecological Environment for Production

It would be nice to suppose that physical factors such as water temperature are likely to generate independent (serially uncorrelated) variations in production processes from year to year. The folly of this supposition has been repeatedly noted in the recent literature, perhaps most forcefully by Cushing (1982). Many climatic factors display some sort of structured variation (trend, pseudo cyclicity, etc.) on every time scale of interest in fish population dynamics. For many major fisheries there has been heated debate about the relative importance of climatic variation as opposed to changes in stock size as a cause of rate variation and apparent response to management measures (Skud 1975, 1982, 1985; Walters 1985a). Of particular concern in stock assessment are climatic changes that occur on time scales of 20–40 yr; we must often examine stock and rate data on this time scale in order to see highly contrasting stock sizes, and the effects on rates of the stock size change may be confounded with effects of the climatic change.

Biotic environments for production (prey resources, competitor abundances, predator abundances) can also vary nonrandomly on a variety of time scales. Some biotic variables, such as zooplankton abundances, should adjust rapidly from year to year in response to physical factors and levels of predation; such "fast variables" (Clark et al. 1979) are unlikely to cause nonstationarity on longer time scales (i.e. planktivorous fish life span) except insofar as they transmit nonrandom variation in physical factors or abundance of longer lived predators. A more troublesome pattern of nonstationarity may be caused by species such as the Great Lakes forage fishes (smelt, alewife, chub, perch) that have life spans of several years; even if recruitment and survival rates for these species vary randomly from year to year, extreme rate events (e.g. large year classes) will cause

abundance changes that persist for at least a few years, so as to produce a pseudo cyclic pattern of competitive impact and resource availability to piscivores. From the standpoint of stock assessment on short-lived fish species, long-lived piscivores (along with some avian and mammalian predators) may cause nonstationarity on the same time scales (20–40 yr) as the troublesome climatic changes mentioned in the previous paragraph.

In contexts such as the Great Lakes, it may seem like nit-picking to talk about pseudo cyclic sources of nonstationarity when there have been large, obvious, and apparently irreversible changes due to introduction of exotic competitors and predators. The large changes of course imply that assessment data more than 10–20 yr old cannot be trusted as a basis for predicting future patterns. The trouble is that there are likely to be potentially misleading patterns of change even within that 10–20 yr assessment "window"; the recruitment rate changes documented by Brown et al. (1987) for the bloater chub (*Coregonus hoyi*) are a good example.

Some biotic sources of nonstationarity, particularly predation effects, can be explicitly represented using large-scale trophic models (Bax and Levastu 1987; Daan 1987). However, such models have massive data requirements often involving species for which historical monitoring data are lacking (e.g. species that have not been of commercial or recreation interest). Even if monitoring programs are instituted immediately to fill such gaps, it will be many years before the large models can be confidently tested against empirical experience.

History as Reflected in Stock Composition

Individuals in natural populations can be grouped by a variety of classification measures (age, spawning location, size, etc.) into relatively homogeneous classes with regard to parameters such as recruits per spawner and survival rate. Suppose the number of individuals in composition class i is N_i, and the average of some rate for individuals in this class is r_i. Then the mean rate $\bar{r}$ over all individuals in the stock is given by

$$(1) \quad \bar{r} = 1/N \sum_i r_i N_i$$

where N is the total stock size. Letting the proportion of individuals in class i be $p_i = N_i/N$, eq. (1) can be rewritten as simply as

$$(2) \quad \bar{r} = \sum_i p_i r_i.$$

From this equation it is obvious that changes in stock composition (as measured by the p_i) can influence the functional relationship between $\bar{r}$ and N, even if all the class-specific rates r_i remain constant over time or are simple functions only of N. It is important to note that eq. (2) applies to *all* definitions of composition classes, whether detailed or coarse. There is no way to be assured of stationarity of the r_i just by using finer classes i, since eqs. (1) and (2) apply to subclasses within N_i as well, and subclass proportions may change over time.

Harvesting and other disturbances are bound to affect the stock classes N_i differently, and the p_i at any moment in time will reflect the history of disturbances. Such effects go far beyond the obvious shifts in age composition that are often included in models. Less productive and/or more vulnerable classes of animals, for which the p_i will decrease under increasing stress, are also created by genetic variation and by a host of factors related to the spatial heterogeneity of the environment over which the stock is distributed.

As noted eloquently by Ricker (1973), the general effect of high exploitation rates is to cause the unfished equilibrium stock size (or logistic carrying capacity stock size k) to decrease over time and the average productivity (recruits/spawners, survival rate, etc.) to increase unless the more productive substocks (classes) are also less vulnerable to fishing. A good recent discussion on changes in substock structure and recruitment associated with fishery development on a species other than salmon, Atlantic herring (*Culpea harengus harengus*), is given in Sinclair et al. (1985). In the Great Lakes context, there will likely be erratic changes in recruitment parameters for species that were nearly driven extinct during the period of peak fishing and lamprey abundance, as these species rebuild and recolonize spawning and rearing areas in an unpredictable pattern over time (think of the p_i in eq. (2) as proportions of a stock that spawn/rear/home to various spatial areas within some larger stock management unit).

Changes in production parameters due to changing stock composition can never be fully explained, anticipated, or controlled by increasing the spatial and biological resolution of sampling programs and regulatory policies. No matter how finely the units of monitoring and regulation are divided, there will still exist compositional complexity within each unit. Also, when there are practical constraints such as a limited total budget for monitoring and for enforcement of regulations, the quality of information and precision of control for each unit may decrease drastically if too many units are managed separately.

Tests for Nonstationarity

While it is easy to identify various reasons why production relationships should change over time, there are also some reasons to expect stationarity (e.g. compensatory nonadditivity of mortality rates due to various agents) and there are a few long-term data sets that indicate surprisingly little change (e.g. the stock–recruitment relationship for Skeena River sockeye salmon has apparently not shifted greatly since the early 1900's despite considerable changes in substock structure, spawning habitat, and harvest patterns). Detailed process research and modelling cannot resolve whether (or why) there has been nonstationarity because there are simply too many possible mechanisms that might dampen or exaggerate the changes. It is therefore wise to empirically examine historical abundance/production time series for evidence of change, without wasting much time in the development of a priori arguments (models) about what to expect. This section reviews a few statistical tools for conducting such examinations.

There is one fundamental requirement for all tests of nonstationarity based on historical data: the data set must not consist only of a "one way trip" (Hilborn 1979) in which the stock size is increasing or decreasing (or constant) over the entire period of record. In such cases, responses (recruitment rates, etc.) are measured only once at most stock sizes, and it is not in principle possible to decide whether observed rate changes have been due to the stock size change or to parameter changes that would result in different rates if the same stock size were sampled a second time. Unfortunately, most fisheries data sets are such one-way trips, either by deliberate design involving regulation to prevent rapid changes in harvest or because monitoring programs have simply not been in place long enough to see several major swings in abundance.

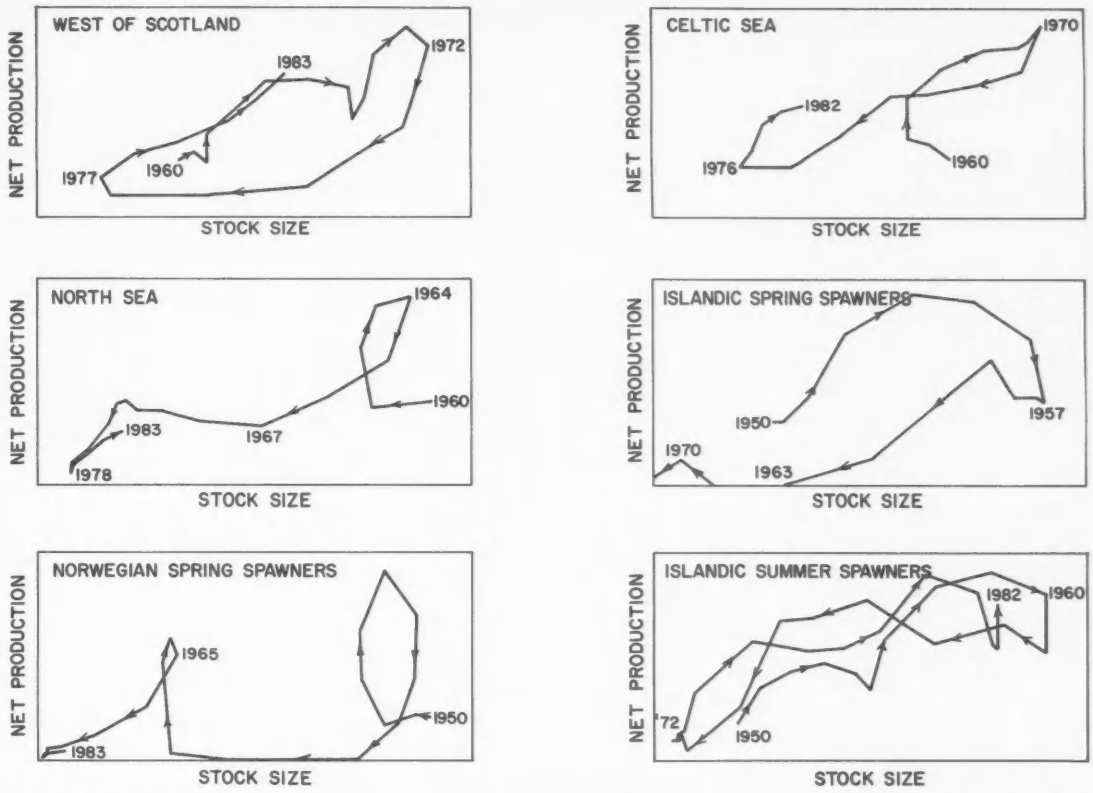

FIG. 1. Relationships between surplus production and stock size for Northeast Atlantic herring stocks, estimated from the stock assessments of Jakobsson (1985). The procedure for estimating surplus production is described in the text.

It is easy to find data sets involving one-way trips for which fitting the data using some particular production model leads to residuals (prediction errors) that change systematically over time. Such systematic changes cannot be used as evidence of nonstationarity during one-way trips, since they may simply be due to the wrong choice of model structure. For example, a logistic (quadratic) production model may nicely summarize net rate changes during the early part of a stock decline, but this model may then overestimate production rates later when stock sizes are lower and depensatory mortality losses are higher, or else underestimate production rates if there are strong compensatory increases in recruitment rate when the stock is lower.

Subjective Indicators of Nonstationarity: Hooks and Loops

Figure 1 shows a collection of relationships between surplus production and stock size, estimated from Jakobsson's (1985) review of stock size (estimated by virtual population analysis (VPA)) and catches in Atlantic herring stocks. To obtain these estimates, I simply assumed that stock biomass B changed according to $dB/dt = P_t - C_t$ where P_t is net production rate and C_t is catch rate. I obtained a smooth estimate $\hat{B}_t$ of dB/dt over time for each stock by fitting a cubic spline to B versus t data and taking a three-point moving average on the resulting point estimates of dB/dt for each year t. P_t was then estimated for each year t as $P_t = \hat{B}_t + C_t$. This estimation procedure is not defensible as a method for analysis of short-term changes in production rates, since it ignores delays and possible errors in the VPA estimate of B, but it should give a reasonable picture of changes in average production rates over time scales longer that 3–5 yr.

Three of the stocks in Fig. 1 represent one-way trips as defined above (North Sea, Norwegian Spring, Celtic); there are not enough repeat observations at different stock sizes to draw any conclusions about stationarity. At the opposite extreme, the Icelandic summer-spawning stock represents a "three-way trip" (increase, decline, increase), and the surplus production relationship was remarkably similar during all three periods. The other two stocks (west of Scotland, Icelandic spring spawners) show a pattern that I call the "loop," in which low production rates during stock decline are followed by higher production rates *at the same stock sizes* during stock increases. In these two cases, stock size alone is clearly not a good predictor of surplus production. The three one-way trip stocks show weak evidence at low stock sizes of another qualitative pattern that I call the "hook," in which production rates during a decline are followed by persistently lower (or higher) rates at comparable stock sizes during a subsequent stock recovery. In these cases, the apparent hooks may simply be early parts of loops as seen in the Scotland and Icelandic stocks.

Based on various examples such as the Atlantic herring, I recommend a three-step strategy for qualitative analysis of

possible nonstationarity in historical time series:

(1) Develop a time series "reconstruction" of stock sizes and rates (recruitment, total surplus, etc.) at whatever degree of biological resolution is feasible with the data at hand, using any estimation method (VPA, stock reduction analysis, etc.) that appears defensible.

(2) Filter the rate time series to remove (or at least reduce) effects of short-term ("random") variation due to environmental factors and measurement errors, using moving averages if the stock size changed smoothly over time, or block averages over years of relatively similar stock size if the stock size showed large and abrupt changes.

(3) Plot the filtered estimates versus stock size and/or relevant functions of stock size such as total egg depostion, labelling the time series points as in Fig. 1 so that directions of change are evident in relation to any hooks or loops that indicate long-term nonstationarity.

Step 1 above is obviously the most difficult and should involve comparison of several estimation methods, since some (especially VPA) may introduce spurious trends or smoothing in the data through factors such as ageing errors in catch at age data. Care is also needed at step 2, since smoothing procedures can introduce spurious short-term trends (hooks, loops) into the smoothed data for years surrounding unusual events (strong year classes, rapid collapses, etc.). Step 2 should be omitted entirely in situations where there has been rapid, stochastic variation in both stock sizes and rates (e.g. stock–recruitment analysis for productive, semelparous species such as salmon), in favor of the more formal statistical procedures discussed below.

Statistical Tests for Nonstationarity

Qualitative analysis as described above and illustrated in Fig. 1 can sometimes provide vivid evidence of long-term nonstationarity. However, it can provide misleading pictures in contexts where there is considerable short-term (less that one fish generation) variability and/or abrupt changes in stock size, and it cannot be used in contexts where the functional relationships of concern involve several variables (e.g. numbers at several ages) and hence cannot be represented graphically without unwanted simplification. There are at least three approaches to detecting and assessing the statistical significance of changes that are not obvious from qualitative analysis: (1) covariance analysis in time blocks; (2) representation of parameters as polynomials in time; and (3) time series analysis of model residuals (prediction errors).

Covariance analysis in time blocks can be performed using the same standard programs for linear and nonlinear regression analysis that are usually used for parameter estimation in unblocked data. The data are first assigned to time blocks, using either arbitrary and fixed block lengths or natural time blocks representing periods of similar transient behavior (e.g. the Icelandic summer herring data in Fig. 1 could be grouped into three blocks, representing the two increase phases and the decline phase). Some caution is needed here, since natural blocking based on prior inspection of the data will result in exaggerated estimates of changes; natural "accidents" involving chance runs of unusual environmental conditions will be ascribed some significance, although they will not likely be repeated in the future. Next, whatever regression model(s) would ordinarily be used to analyse the unblocked data is extended to include new parameters representing variation among blocks, and the extended model is fitted to the data. For example, stock–recruitment analysis is often based on the Ricker model, with parameters a and b estimated by the linear regression $y = \log(R/S) = a - bS$ (R = recruits, S = spawners or egg deposition; for warnings about this procedure, see Walters 1985b). This model can be rewritten as $a + a_i - bS - b_iS$ where a_i and b_i are block i effects constrained so that $\Sigma_i\ a_i = 0$, $\Sigma_i\ b_i = 0$; the extended parameter set is $[a, b, a_1,\ldots, a_{n-1}, b_1,\ldots, b_{n-1}]$ where n is the number of blocks. Finally, standard significance tests for comparison among linear model parameters are applied using the estimates and their covariance matrix. Such tests may overestimate the significance of differences, since the data from within each block are time series with possible autocorrelations (even if arbitrary rather than natural blocks are used), but such errors are conservative from a management standpoint (i.e. it is better to be prepared for large changes than to pretend stationarity).

When there is suspicion that production parameters have been changing smoothly over time, so that blocking of the data into presumably homogeneous periods would be inappropriate, the parameters may be represented as time polynomials in the context of regression analyses. Again using Ricker stock–recruitment analysis as an example, we might represent the log (R/S) regression as $Y_t = a_0 + a_1t + a_2t^2 - b_0S_t - b_1S_t t - b_2S_t t^2$. Here, a_1, a_2, b_1, and b_2 represent temporal changes in a and b. This approach makes it obvious why parameter changes cannot be detected in one-way trips: if S_t has decreased linearly (or quadratically) over time, then the whole regression reduces to (cannot be distinguished from) a simple polynomial regression in t, with polynomial coefficients representing confounded combinations of the desired a_i and b_i. The approach has been used to study temporal changes in catchability coefficients in catch at age models (Fournier 1983), but to my knowledge it has not yet been applied to the analysis of growth or recruitment data.

A third approach is to fit production models to the data while assuming stationarity of parameters, then use various tests to show that the residuals are uncorrelated with stock size (possible model structure errors), and then finally plot the residuals over time and use time series analysis to detect and determine the significance of any nonrandomness in the series. An example of this approach is shown in Fig. 2, where I plot results of Wong's (1982) analysis of Fraser River sockeye salmon. The "stock" in this case is a mixture of very distinct spawning races, mostly having a fixed 4-yr life cycle. This cycle is obvious in the recruitment and spawning stock time series, but data from the four cycle years appear to be randomly scattered around a single, average stock–recruitment relationship. When a Ricker model is fitted to this relationship, the residuals from the log (R/S) = $a - bS$ regression show a temporal pattern involving runs of good and bad years, but no 4-yr cycle. The autocorrelation function for the residuals supports this conclusion (significant lag 1 correlation, no other significant correlations). However, analyses of time series data for individual Fraser sockeye races (Walters and Staley 1987) have not given results comparable with Fig. 2; the major races do not show clear runs of above and below average productivity for the same years as indicated in the residuals time series plot of Fig. 2. Hence, the residuals pattern in Fig. 2 may represent nonstationarity in stock composition rather than an "environmental effect" shared by the stocks.

It has become standard practice in fisheries stock assessment to seek correlations between residuals from population models

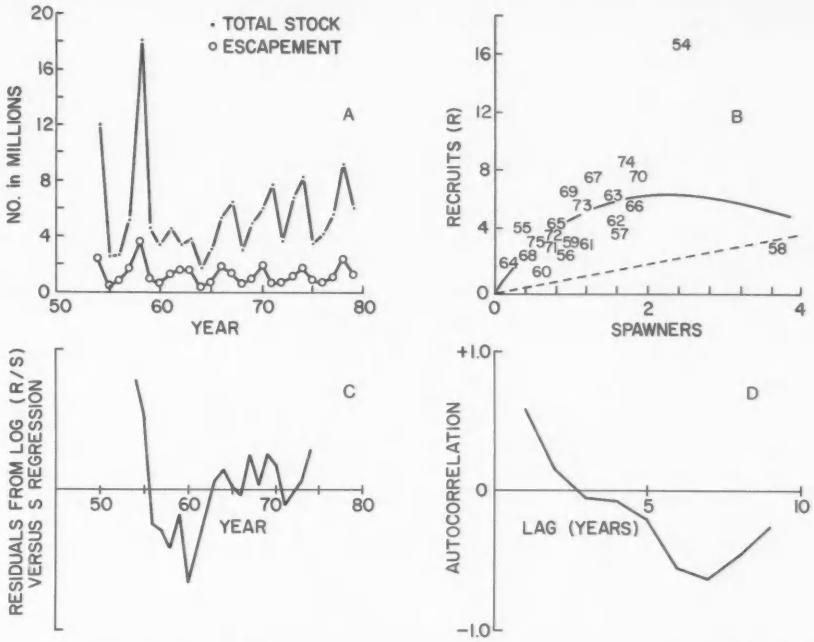

FIG. 2. Stock and recruitment statistics for Fraser River sockeye. (A) Time series of stock sizes and escapements; (B) relationship between escapement in year t and resulting stock in year $t+4$; (C) time series of deviations from stock–recruitment relationship in Fig. 2B, measured as deviations from regression of log (N_{t+4}/S_t) on S_t; (D) autocorrelation function for deviations from Fig. 2C (only the lag 1 autocorrelation is statistically significant). (From Wong 1982)

and various environmental factors, in hopes of identifying causal mechanisms for the variation. The utility of this practice in management contexts is questionable (Walters 1985a), and it can obviously be misleading in research contexts. A point that is often overlooked is that even if an environmental correlation is not spurious, the environmental factor will induce stock size changes whose effects will in turn be difficult to separate from later environmental effects (unless exactly the right model for stock size effects is used in the first place, a highly unlikely possibility). Rather than agonize over causation of variation that cannot be controlled (or predicted even given causation, since the environmental factors usually recognized as causes of variation are not themselves predictable), it appears more useful to seek statistical descriptions of the variation (through time series models, analysis of variation between time blocks, etc.) and look directly at the implications of this variation in terms of feedback management policies.

Harvesting Policies for Nonstationary Systems

A basic implication of nonstationarity in rate versus stock size relationships is that stock size and exploitation rate targets should be adjusted over time through regular analysis of monitoring data; there has been little research on the optimum design of such adaptive feedback strategies. As I shall indicate in this section, the policy design problem involves much more than issuing a few platitudes about the need to adjust parameter estimates and harvest rates over time.

There are two extreme cases or situations in relation to the ability of a management system to detect and react to evidence of nonstationarity. In the "fully observable" case, the average long-term production relationship is known with confidence, and it is possible to measure each year the status of the stock with respect to deviation from the average. The Fraser sockeye example (Fig. 2) comes close to this case: the long-term stock-recruitment relationship appears to be stable, and the residual from this relationship can be determined each year from the stock size, escapement 4 yr previous, and the average stock–recruitment parameters. At an opposite extreme is the case that I term "fully adaptive" in which there is no evidence of a stable long-term relationship and the effects of past nonstationarity are confounded with the effects of stock size changes. One-way trips fall in this category, as do stocks for which only limited "hook" or "loop" pattern data have been acquired (most stocks in Fig. 1 are good examples). The following discussion will focus mainly on the fully observable and fully adaptive extreme cases, since little is understood about these cases from optimization studies using stochastic dynamic programming.

Dynamics Fully Observable

Suppose that there are enough historical data to demonstrate convincingly (a subjective judgement!) that the stock dynamics follow a basic functional relationship

$$(3)\quad N_{t+1} = f(S_t, \beta, w_t)$$

where N_{t+1} is a vector of stock size measures prior to harvest in year $t+1$, S_t is a vector of stock measures after harvest in year t,

β are parameters of the function, and w_t is deviation from the average production relationship defined by β. If the dynamics are nonstationary, w_t may show long runs of above or below average values (see residuals plot in Fig. 2) that reflect a variety of changing biotic and abiotic influences on the stock. Suppose further that the relationship f is invertible in w_t, so that $w_t = f^{-1}(N_{t+1}, S_t, \beta)$ can be computed once N_{t+1} and S_t have been observed. This is the observable case, defined a bit more precisely. There is no objective way, even given hundreds of years of data, to be absolutely confident that the mean relationship is stable or could not be more accurately described by some alternative structure f' or parameter combination β'; thus, f and β must be viewed as a working hypothesis to be used in policy design until some better formulation (with smaller, less structured w_t) is discovered.

There is a growing literature on optimum harvest policies for situations where w_t is white noise (time covariances zero); for recent reviews, see Clark (1985) and Mangel (1985). The basic conclusion from this research has been that the optimum harvest policy is a stationary feedback function $h(N_t)$ that specifies the harvest to take in year t as a function of the stock size that year. If the management objective is to maximize long-term harvest, h is a "fixed escapement" policy. If the management objective is risk averse (avoid low harvests, reduce harvest variability), then h will usually be closer to a fixed exploitation rate (Deriso 1985).

To understand how nonstationarity affects optimum policies in the fully observable case, I conducted a series of optimization trials using stochastic dynamic programming and some simple prototype models for f involving only total stock size and escapement. These models were of the forms

variable survival:

$$N_{t+1} = \begin{cases} w_t S_t \text{ if } w_t S_t < k \\ k \text{ if } w_t S_t \geq k \end{cases} \tag{4}$$

variable capacity:

$$N_{t+1} = \begin{cases} aS_t \text{ if } aS_t < w_t \\ w_t \text{ if } aS_t \geq w_t. \end{cases}$$

These are rectilinear stock–recruitment (or surplus production) models. In the "variable survival" model, w_t represents the (variable) population growth rate at low stock sizes. In the "variable capacity" model, the growth rate is fixed at a for low stock sizes, and w_t represents (variable) carrying capacity or maximum stock level. For both models the objective "maximize average harvest $N_t - S_t$" is accomplished by leaving a fixed escapement S^* if w_t is fixed ($S^* = k/w$ for variable survival; $S^* = w/a$ for variable capacity). To simulate nonstationarity, I allowed the w_t to take a series of discrete values (e.g. 3, 5, and 7 to represent poor, average, and good carrying capacity) and assumed that w_t changes from year to year according to a simple Markov process:

$$\begin{aligned} &\Pr(w_{t+1} = w_t) = P_s \\ &\Pr(w_{t+1} = w' \neq w_t) = (1 - P_s)/(n - 1) \end{aligned} \tag{5}$$

where n is the number of discrete environmental states. Here, P_s is simply the probability that the environment at $t+1$ will remain the same as at x, and all environmental changes are assigned equal probability $(1 - P_s)/(n - 1)$. Stationarity corresponds to $P_s = 1/n$, while larger values of P_s represent progressively less common but more persistent shifts between environmental states. I also examined more complex hypotheses for environmental transition and obtained results essentially the same as for eq. (5).

TABLE 1. Optimum escapements for a simple stock–recruitment model with a time-varying carrying capacity and different probabilities P_s that the carrying capacity will be the same next year as this year. Tabled numbers are the optimum escapements on a stock size scale of 0–32. k is the carrying capacity as defined in eq. (4). Note that the optimum choice is escapement = 7 for all environmental states only when P_s implies nearly stationary dynamics ($0.25 < P_s < 0.5$).

Probability of environmental state persisting	Current environmental state		
	Poor $k = 12$	Average $k = 20$	Good $k = 32$
$P_s \geq 0.75$	3	5	8
$0.5 < P_s < 0.75$	5	5	8
$P_s = 0.5$	5	5	7
$0.25 < P_s < 0.5$	7	7	7
$P_s \leq 0.25$	7	7	5

For the prototype models as described by eqs. 4 and 5, the optimum policy (maximize average $N - S$) is still a stationary, fixed escapement feedback function, but the optimum escapement S_t^* may depend on w_t (optimum in relation to N_t is to harvest nothing if $N_t \leq S_t^*$, and harvest $N_t - S^*$ if N_t exceeds S_t^*). The dependence on w_t is shown in Table 1 for a sample calculation with the variable capacity model (with $a = 4$); similar results were obtained with the variable survival model. Essentially, I found that the optimum policy is to *ignore* future changes in w_t provided P_s is large enough (>0.75 in the Table 1 example) and to choose less extreme escapements (than implied by w_t = constant) when the likelihood of change is large. When all environments are equally likely (w_{t+1} independent of w_t), S^* of course becomes independent of w (row of 7's in Table 1). When there is a very low probability of staying in the same state ($P_s \leq 0.25$), the optimum policy is to anticipate a return to average conditions when the current environmental state is above average (choice of 5 in the last row of Table 1). Similar results to Table 1 are obtained when the number of distinct environmental states is increased (I have tested up to 10): slow transitions (high P_s) imply ignoring future changes, while rapid transitions (low P_s) imply acting as though there were a single recruitment relationship with random variation around it.

As a variation to the theme of eq. (5), I computed optimum policies for cases where the environmental transition probabilities are biased in one direction, so w_{t+1} either stays the same as w_t or moves to the next more (or less) favorable state with probability $1 - P_s$. In such cases, the optimum policy turned out to be either to ignore the future changes (for high P_s) or else act as though the next more (or less) favorable state were going to occur at $t + 1$ and then persist into the future. I could not find parameter combinations for which the optimum policy involved anticipation of changes for more than one step into the future.

It appears to be generally true for the fully observable case, with harvest rates fully controllable, that the optimum policy is "myopic" and involves pretending either that (1) the current environmental state will persist indefinitely, (2) when a trend is evident, then the next environmental state in this trend will persist indefinitely, or (3) when the persistence (P_s) of environmental states is low, then future states will occur at random. It is

a difficult problem to analytically prove the generality of the myopic assertation, but I predict that applied mathematicians will soon provide useful insights about this problem.

The assertion that optimum policies are myopic for the fully observable case may prove false in an important class of situations, namely where the year-to-year change in harvest rates is tightly constrained due to concern for socioeconomic stability (Walters 1978). It is difficult to compute optimum policies for these situations (since the last harvest $N_{t-1} - S_{t-1}$ becomes an additional state variable besides N_t and w_t), but it could be that the constraints imply a need to look further into the future than 1 yr when clear trends in w_t are evident. When examined closely, many arguments about the need for long-range planning in fisheries are based on well-founded fears that policy changes will be difficult and slow to implement. There is a real need in fisheries science for careful analyses of the dynamics of the political bargaining processes through which harvest policy changes are determined, so that optimization models with realistic and defensible constraints can be developed.

The Fully Adaptive Case

The fully observable case discussed above does arise in fisheries practice, but it is much more common to have only limited experience with average production responses, so that production rates can at best only be predicted with confidence for a narrow range of stock sizes "sampled" through recent management experience. Perhaps the most prevalent decision making context in fisheries today is where the stock has been depleted through a one-way trip of fishery development and perhaps natural accidents, and the issue is whether to cut back on harvests so as to allow a recovery to levels that the historical data indicate might be more productive. In defence of the rebuilding policy, one might point to examples such as the Icelandic summer-spawning herring in Fig. 1, where recovery has led to increased productivity. In contrast, interest groups who stand to lose by harvest cutbacks might point to examples such as Pacific herring (*Culpea harengus pallasi*) in northern British Columbia (Walters et al. 1982), where recruitment rates have not recovered to historical levels following collapse of a reduction fishery in the 1960's.

In most fisheries, it is unreasonable to hope that "natural experiments" will regularly provide an informative range of stock sizes for statistical analyses, and in any case the results from such analyses are likely to be misleading (Walters 1985a). *Thus the key issue in the actively adaptive case is whether it is worthwhile to periodically conduct deliberate experiments involving stock size manipulations*, so as to pin down production relationships that may be changing over time at rates that are fast enough to "track" but not so fast as to be modelled as just noise. This is fundamentally not a biological issue; instead it is one of socioeconomic valuation of policy choices in the face of uncertainties that no amount of ecological research and argument can resolve without actually seeing the results of informative stock size variations. Extrapolation from past experience or ecological principles is easy enough, but in the end, it is risky to trust such extrapolation, and it is a matter for economic and political analysis to decide whether the risks are worth taking.

Two decision making approaches are possible in the fully adaptive cases. The *passively adaptive* approach is to ignore nonstationarity and pretend knowledge of production relationships based on intuition or past experience, and then rely on learning to occur through the inadvertent management mistakes and natural variations that will inevitably occur. The *actively adaptive* approach is to deliberately look forward in time at the impact of current decisions on future uncertainty and possible mistakes arising from that uncertainty, and then select decisions that balance the value of reduced uncertainty against any immediate costs or losses that the decisions may entail. The actively adaptive approach views every decision choice as an experiment with uncertain outcome and an implicit "information value" that depends on how far the choice departs from historical practice (how large a range of stock sizes will be sampled if the choice causes departure from recent historical trends).

Some basic factors that determine whether experimentation is worthwhile, given that there is substantial uncertainty about optimum stock size, are (Walters 1986) as follows:

(1) Level of random variation, due both to natural factors and monitoring procedures, in response to stock change. (Can a definitive result be obtained quickly?)

(2) Discount rate on value of future harvests. (Are long-term gains valuable in comparison with short-term losses due to experimental harvest variation?)

(3) Degree of economic dependence or specialization on the target stock. (Can fishermen and related enterprises switch to other stocks or activities during the experiment, so as to spread their costs and risks?)

(4) Applicability of the experimental results to other stocks. (Can losses on one or a few stocks be justified in terms of improved management for many others?)

Integrating these factors into a common framework for computing optimum policies is a difficult problem, which has not yet been solved for fishery situations. In particular, there is no general agreement even about how to begin analysis in terms of an objective function to be optimized (what are reasonable discount rates, how to weigh alternative outcomes through probabilities and utility measures, how to measure the complicated secondary economic impacts of changing harvests, etc.). Even given a reasonable objective function and set of alternative hypotheses about experimental outcomes, there is a major computational difficulty that has not been overcome: the optimization calculations must anticipate not only a variety of possible ecological/economic responses, but also the future learning process (data gathering, reestimation of parameters, modification of policies based on new assessments). This is a tall order, and computational experience to date has been discouraging. However, one important point has emerged from this experience to suggest that further research in the area is important: scientific intuition is a very poor guide in estimating the value of experimentation, since it is difficult to divorce the desire to satisfy scientific curiosity from the desire to provide information that is truly necessary or relevant to policy formulation. It would be really interesting to drive some populations very low so as to measure depensatory mortality effects of natural predators, but a sound management system would never allow such low stock sizes in the first place.

Simple optimization formulations have suggested (review in Walters 1986) two main qualitative conclusions about optimum policies in the face of nonstationarity, when the conditions listed above are favorable to experimentation in the first place (rapid learning, low discount rate, low economic dependence). First, management choices in connection with natural changes gener-

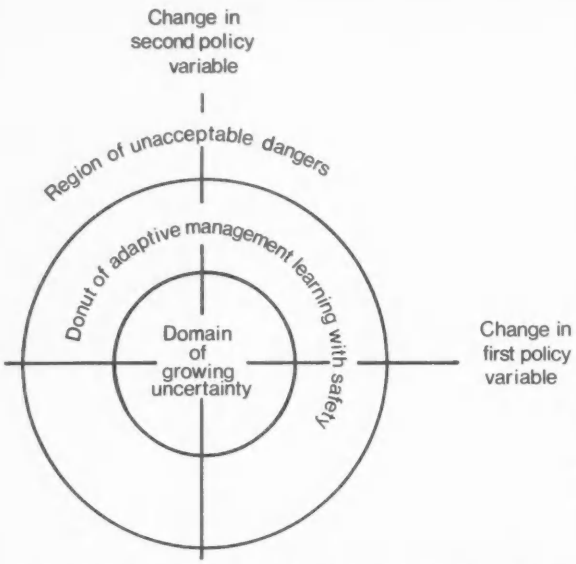

FIG. 3. Changes in management policies and stock size involve a donut of choices. For small changes, uncertainty is increasing over time due to nonstationarity, to form the donut hole. Large, unacceptably risky changes define the outside of the donut. (From Walters 1986)

ate a "management donut" (Fig. 3) in relation to variation around the recent historical state of affairs. On the one hand, if management actions and natural factors induce too little variation in stock size, the system operates in a domain (the donut hole) of growing uncertainty over time. On the other hand, very large disturbances involve unacceptable risks, and these disturbances define the outside of the donut. The donut itself represents combinations of policy changes that are enough to at least prevent uncertainty from growing, but not so large as to be unacceptably risky. The second main qualitative conclusion is that small ("dithering") experimental changes are not worthwhile: it is better to remain uncertain than to introduce small changes that cause deterioration in short-term harvest value without resulting in clear discrimination among alternative hypotheses about production relationships. Dithering policies may not even be adequate to prevent uncertainty from growing over time (i.e. to move outside the donut hole of Fig. 3). The second conclusion has an interesting implication for long-term management in nonstationary systems: the optimum policy may involve episodes of strong experimentation (probing, exploratory management behavior), alternating with periods of more cautious, stabilizing management activity (Fig. 4).

Expected gains from following actively as opposed to passively adaptive policies have been calculated for a few situations involving uncertainty about stock–recruitment or surplus production parameters (Smith and Walters 1981; Ludwig and Walters 1982; Ludwig and Hilborn 1983; Walters 1986). These calculations indicate that the expected gains, when measured in terms of average long-term yield, will rarely exceed 20% with the typical improvement from active policies being more like 5–10%. However, active policies are much less likely to result in gross blunders, where the stock is managed at far below optimum levels for long periods. Also performance improvements from active policies are greater in situations

FIG. 4. Adaptive optimization with simple models has suggested that episodic stock disturbances may be the best policy when production parameters are changing unpredictably over time. (From Walters 1986)

where nonstationarity is introduced in a manner that causes little change in the system behavior near the managed equilibrium or target stock size, but instead creates opportunities for improved yield at other stock sizes. For example, changes in ecological carrying capacity will not be evident to a passively adaptive manager who acts to hold a stock at some productive level that was estimated to be optimum using early data (Fig. 5).

There has been considerable debate about the practicality of implementing experimental, actively adaptive policies. Such policies are currently in use for two Pacific salmon stocks (Rivers Inlet sockeye in British Columbia and Quinault River chinook in Washington); in both cases there has been agreement to reduce exploitation rates, at least on larger runs, to test the effects of increased escapement. Plans are being developed to apply similar policies on major Fraser and Columbia River stocks. It is still too early to say whether there are any unexpected, catastrophic consequences (biological, economic, or political) of introducing episodes of large-scale experimentation into the management process. A major concern has been that admissions of ignorance (uncertainty) by management authorities will lead to a loss in their credibility to the fishermen, and hence to political battles that result in anarchy with no management policies being politically acceptable. The experience to date suggests that this concern is unwarranted and is indeed based on a false premise that management authorities have much credibility in the first place. With the development of various advisory and comanagement procedures, through which fishing industries can bring forth independent assessments and expert advisors, fisheries management agencies across North America are being forced to admit and confront uncertainties that a few years ago would routinely be hidden in reams of tabled statistics and charts. Various councils and advisory boards will perhaps provide the main crucible through which wise adaptive management plans will be developed in the near future.

Conclusion

Nonstationarity in production relationships should be a matter of central concern in stock assessments based on historical time series data. There is a need to develop better qualitative and formal statistical procedures for detecting nonstationarity. When the nonstationarity is measurable (observable) in terms of patterned deviation from some long-term average relationship, it is possible to design a feedback policy that specifies target harvest rates or stock size as a function of the deviation; usually this policy will involve managing as though the current deviation were going to persist indefinitely. When there is not enough historical experience to precisely

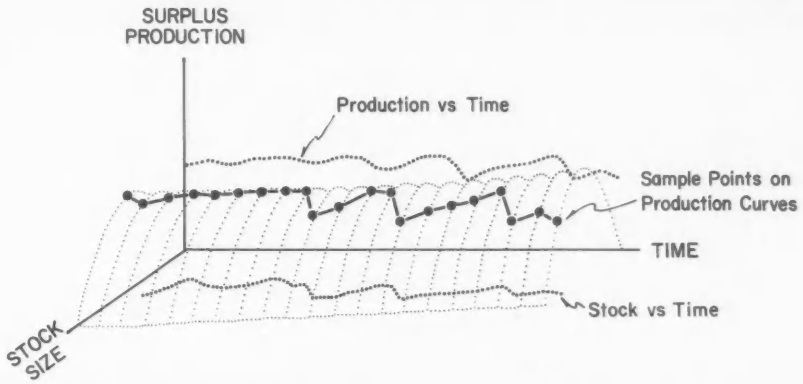

FIG. 5. Under a passively adaptive policy, the sampled trajectory of stock sizes and production rates may not provide clear signals that the production relationship is nonstationary. In this example, the surplus production function is becoming steeper (higher population r value) while the carrying capacity stock level (population k) is decreasing, as might be expected due to loss of less productive substocks over time. In later years, the stock size is maintained at higher levels than would maximize surplus production.

characterize the nonstationarity, then there is a difficult policy choice between passively waiting for informative stock changes versus actively experimenting with harvest rates to more quickly test responses over a range of stock sizes. Actively adaptive policies, involving episodes of strong stock size disturbance, should theoretically result in higher average yields over the long run. However, such policies are not optimum in contexts where decision making is dominated by interest groups whose main concerns are short-term yields and temporal stability of yields.

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Potential *Stizostedion* Yield as a Function of Chlorophyll Concentration with Special Reference to Lake Erie

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Models for predicting potential fish yield from indices of productivity or standing crop at a lower trophic level have proved most reliable when applied to a specific fish association. Using chlorophyll concentration as the independent variable, we demonstrated that *Stizostedion* yield was defined by a dome-shaped curve with maximum catch of about 10 $kg \cdot ha^{-1} \cdot yr^{-1}$ occurring between 7.5 and 12.5 mg chlorophyll $a \cdot m^{-3}$. We postulate that the ascending and descending portions of the curve represent trophic regions where walleye production is replaced, respectively, by that of salmonid/coregonid- and centrarchid/cyprinid-dominated communities.

Les modèles permettant de prédire le rendement potentiel de poisson à partir d'indices de productivité ou de biomasse à un niveau trophique inférieur se sont avérés fiables lorsqu'appliqués à une association particulière de poissons. En nous servant de la concentration chlorophyllienne comme variable indépendante, nous avons démontré que le rendement de *Stizostedion* était défini comme une courbe en forme de dôme, les prises maximales d'environ 10 $kg \cdot ha^{-1} \cdot an^{-1}$ se produisant lorsque la teneur en chlorophylle *a* se situait entre 7,5 et 12,5 $mg \cdot m^{-3}$. Nous postulons que les parties ascendante et descendante de la courbe représentent des régions trophiques où la production de dorés est remplacée respectivement par celle de communautés dominées par les cyprinidés/centrarchidés et les salmonidés/corégonidés.

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Many simple, empirical predictors of fish yield have been developed since Ryder (1965) first proposed the morphoedaphic index. A summary of these is presented in Leach et al. (1987). Most predictive models have been derived by regressing total catch of all species on indices of productivity, and the majority were developed for and are applicable to north temperate latitude lakes. For purposes of fishery management, lack of precision and inability to predict yield of individual species pose the most serious limitations. Precision is enhanced if a specific community is targeted (Jones and Hoyer 1982; Liang et al. 1981).

A reliable estimate of potential yield would be of immediate value to managers concerned with the walleye (*Stizostedion*) fishery of Lake Erie's west basin. Walleye dominate the fishery, and yields have undergone a boom–bust–recovery cycle in recent decades (Hatch et al. 1987). A major current concern is the level of stock which can be maintained without disrupting community structure. Data sets appropriate to trophic index modelling and extending over a period of years are available for the west basin and for Oneida Lake, New York, the site of another highly productive walleye fishery. There are additional extant sets for many Ontario lakes and for two *Stizostedion*-dominated lakes in Sweden. These observations suggest that an opportunity exists for defining a *Stizostodion* – lake trophic status relationship that would be useful in managing walleye fisheries.

The specific hypothesis we set out to test was "Yields of *Stizostedion* from lakes in which this is the dominant piscivore increase as a function of average summer chlorophyll concentration up to some unknown level."

Defining the Variables

Communities having *Stizostedion* (either *vitreum*, the walleye, or *canadense*, the sauger, in North America and *lucioperca*, the pikeperch, in Europe) as their dominant piscivore typically contain such other top predators as northern pike (*Esox lucius*), burbot (*Lota lota*), and smallmouth bass (*Micropterus dolomieui*) (North America) or brown trout (*Salmo* trutta) (Europe). Prey species usually include yellow perch (*Perca flavascens* in North America; *P. fluviatilis* in Europe). Many of these associated species are also harvested with catch composition largely depending on the presence/absence and relative

TABLE 1. Data on surface area (A), mean summer chlorophyll a concentration ([CHL]), and yield (Y) of all species and *Stizostedion*[a] for Ontario lakes, Lake Winnipeg, the west basin of Lake Erie, Oneida Lake, and two Swedish lakes.

Lake	A (km^2)	[CHL] (mg·m^{-3})	Y_{total} (kg·ha^{-1})	$Y_{Stizostedion}$ (kg·ha^{-1})	Reference(s)[b]
Attawapiskat	261.6	2.0	0.5	0.2	1, 11
Loglegged	69.2	2.2	0.7	0.2	1, 11
Wunnummin	235.8	2.4	0.8	0.6	1, 11
Lac des Mille Lacs	241.1	3.6	0.9	0.6	1, 11
Sowden	37.2	1.9	0.9	0.3	1, 11
Nikip	55.2	1.7	1.1	0.3	1, 11
Scugog	70.3	10.7	1.5	0.6	8, 11
Marchington	36.4	1.2	1.6	0.5	1, 11
Weagamow	124.3	2.1	2.0	0.6	1, 11
Winnipeg	23750.0	2.3	2.0	0.5	4, 9
Indian	39.6	2.0	2.5	0.6	1, 11
Doe	11.9	5.4	3.4	1.0	2, 11
Cameron	13.0	1.6	3.8	1.3	2, 5
Nipissing	855.0	1.9	3.9	1.5	3, 7
Lower Buckhorn	12.3	5.9	5.0	3.5	2, 11
Balsam	46.8	2.5	5.6	2.3	2, 11
Sturgeon	43.0	7.0	6.5	4.6	2, 11
Erie (west basin)	3276.0	10.8	17.2	6.5	6, 10, 12
Oneida	206.7	11.1	—	5.0	13
Mälaren	1140.0	14.8	3.4	1.1	14, 15
Hjälmaren	475.0	14.9	4.5	3.2	14, 16

[a]North American lakes *vitreum* and those in Sweden *leucioperca*.

[b]1. Adams and Olver (1977); 2. Anonymous (1982a); 3. Anthony and Jorgensen (1977); 4. G. J. Brunskill (pers. comm.); 5. Dillon and Rigler (1974); 6. Great Lakes Fishery Commission (1978–80); 7. C. R. Jorgensen (pers. comm.); 8. C. A. Lewis and M. A. Henderson (unpubl. data); 9. W. Lysack (unpubl. data); 10. Ohio Department of Natural Resources (1978–80); 11. Ontario Ministry of the Enviroment (internal files); 12. Rathke and Edwards (1985); 13. J. Forney (pers. comm.); 14. Rundberg (1977); 15. Willén (1975); 16. Willén (1976).

importance of commercial and recreational fisheries and/or cultural preferences of fishermen and fish consumers.

After reviewing community composition for a number of systems, we designated as "*Stizostedion* lakes" those for which members of this genus were the dominant piscivore and, where it could be determined, they were not less than one-fourth of total fish yield.

The various empirical models that have been used to predict fish yield are reviewed and their application to Great Lakes fisheries discussed by Leach et al. (1987). One of these, using mean growing season chlorophyll concentration (hereafter designated as [CHL]) as the predictive variable, was selected for our purposes. Choice was based on both empirical and rational grounds. A prime consideration was the availability of comparable data sets extending over time for Lake Erie and spatially for a spectrum of other lakes representing various *Stizostedion* yields and [CHL]. Rationally, the selection of chlorophyll receives support from both food web and particle size theories.

Procedures and Limitations

Trophic-type fish yield estimators so far developed have been based on comparative data representing a set of lakes. Multiple-year data for any member of a set are rare and, where available, have generally been averaged to produce a single data point. Another approach to developing this type of model would be use of long-term sequences of data for a single lake or set of highly similar lakes. Simultaneous limnological and fishery studies on Lake Erie and Oneida Lake have continued over a long enough period to offer such a possibility. Evaluating this opportunity to try a modified approach in trophic-type modelling produced new insights into factors limiting the approach but also resulted in new understandings as described below.

During the period for which data were available, Lake Erie walleye yields were the result of previous overfishing followed by strict management control designed to permit stock recovery (Hatch et al. 1987). The Oneida Lake data sequence presented different problems. Forney (1974) has described how walleye production in Oneida is highly dependent on young-of-the-year yellow perch whose annual variation of abundance is largely determined by abiotic factors. In addition, angler catch, the sole source of yield in this lake, is inversely related to the abundance of yellow perch available as walleye forage. Taken together, these two factors suggest a partial uncoupling of the linkage between the first trophic level and walleye yield.

For the above reasons, pooled multiple lake data sets were relied on for developing walleye yield regressions. However, the multiple-year information available for Lake Erie's west basin proved essential in developing modifications of the simplistic trophic based modelling approach. Data sets used in testing our hypothesis are given in Table 1.

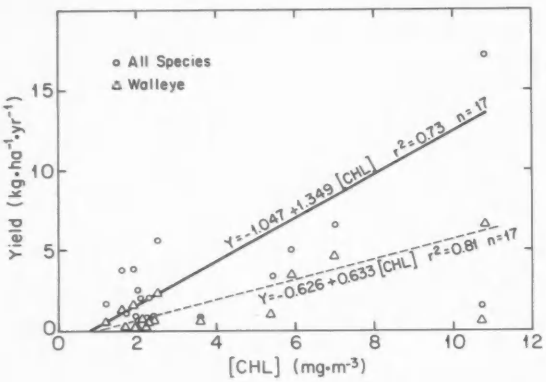

FIG. 1. Regressions of walleye and total fish yield on mean growing season [CHL] for Ontario lakes, Lake Winnipeg, and the west basin of Lake Erie (see Table 1 for data and references). Lake Scugog, Ontario, (lower right-hand points) was omitted from the regressions.

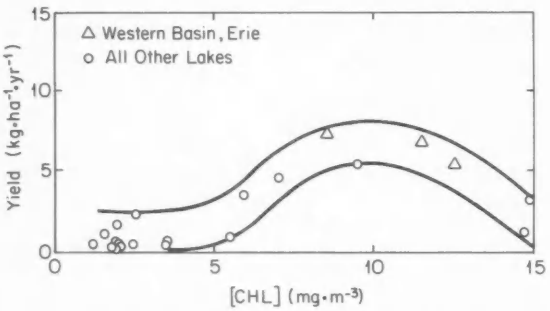

FIG. 2. Distribution of *Stizostedion* yields as a function of mean growing season [CHL] for the west basin of Lake Erie (1978–80), Oneida Lake, Ontario lakes, and Lakes Mälaren and Hjälmaren. Data and sources are cited in Table 1.

Results

Regression analyses of a walleye lake data set, mainly for Ontario lakes, indicated strongly positive correlations of walleye and total fish yield with mean growing season [CHL] when one member of the set, Lake Scugog, Ontario, was omitted (Fig. 1). C. A. Lewis (pers. comm.) regards this lake as underfished because of extensive, dense macrophyte cover. Multiple regressions that included lake area, mean depth, and total phosphorus concentration did not result in significantly higher coefficients of determination.

When the range of [CHL] values was extended with the addition of two eutrophic European pikeperch (*Stizostedion lucioperca*) lakes, when Lake Erie walleye catch was divided into constituent years, and when highly productive Oneida Lake was added, the linear regression shown in Fig. 1 became a first-order curve describing the ascending limb of a dome-shaped curve (Fig. 2). A band, rather than a fitted curve, was used to describe the walleye yield – chlorophyll relationship because we felt that this maximized its immediate utility as a guideline for fishery management.

Lakes on the lower ascending part of Fig. 2 are mainly located in northwestern Ontario, a boreal forest environment scarce in nutrients and with minimal anthropogenic input. Those on the far right of the curve reflect the stress of cultural inputs on the *Stizostedion* community (Leach et al. 1977; Hartmann 1977). As discussed below, we expect that total (all species) fish production may be quite high in these systems, with that of *Stizostedion* replaced by taxa more suited to a eutrophicated environment.

Lake Erie's west basin is of special interest because of both ASPY's focus and its uniquely high walleye production and special management problems. The walleye stock has been under quota management since 1976. Estimated biomass of walleyes in the western basin has increased from 42kg·ha^{-1} in 1976 to about 78 kg·ha^{-1} in 1984 (Hatch et al. 1987). These biomass estimates are in excess of those recorded previously for North American lakes (Carlander 1977; Colby et al. 1979). Sport and commercial harvests in the basin from 1980 to 1985 have ranged from 7.6 to 12.4 kg·ha^{-1} (Ontario Ministry of Natural Resources and Ohio Department of Natural Resources report to the Great Lakes Fishery Commission). The Ontario commercial fishery took from 24 to 45% of those harvests with the balance going to the Ohio, Ontario, and Michigan sport fisheries. Although these estimated yields are some of the highest for walleye in North American lakes, they are probably conservative due to assessment difficulties associated with multiagency management.

There is evidence that density-dependent mechanisms are operating in the population and the stock has extended its range into an adjacent area of the central basin of the lake (Hatch et al 1987). Probably as a result of the increased walleye stock, forage fish availability in the west basin appears to have declined (Knight et al. 1984). There is little evidence that walleye in the basin prey on yellow perch as they do in Oneida Lake (Forney 1974), but the possibility of interaction increases with reduction in alternate prey species. Knight et al. (1984) have suggested increased fishing mortality as a remedial management measure. On the basis of current biomass estimates and a P/B ratio of 20% for adult walleyes (suggested by P. J. Colby, pers. comm.), it is possible that the west basin population could sustain harvests of up to 15 kg·ha^{-1}. Kempinger and Carline (1977) considered that yield should approximate annual production when natural mortality is low and populations are in equilibrium. This consideration is based on records from Escanaba Lake, Wisconsin, where the angling yield of walleyes has averaged 9 kg·ha^{-1}·yr^{-1} for several decades. However, it is doubtful if harvesting at this level could be maintained by naturally reproducing walleye populations in many smaller inland lakes because of habitat restrictions and species interactions. Therefore, the relationship between yield and chlorophyll a, suggested by the dome-shaped band in Fig. 2, may be realistic with the hypothesized maximum yield occurring only in unique environments such as the west basin of Lake Erie.

Liang et al. (1981) hypothesized that the relationship between fish yield and gross photosynthesis could be described with a logistic curve, and they assigned previously published regression equations to portions of the curve. In Fig. 3, we have suggested that a similar curve exists for the fish yield–[CHL] relationship and that it can be roughly apportioned to several taxonomic groups or communities. Considerable overlap between groups occurs. In an earlier aproach, Colby et al. (1972) suggested a relationship between both yield and taxonomic composition and an index of productivity such as the MEI, and Hartmann (1977) has developed a set of such curves for

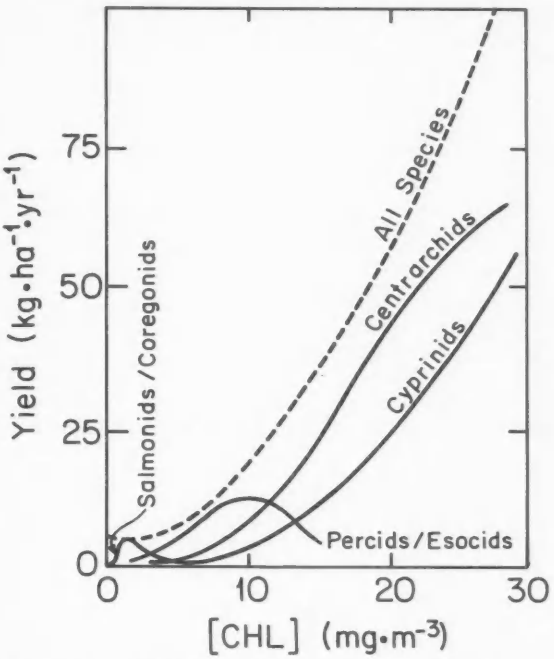

FIG. 3. Estimated distribution of fish yields among major taxa for north temperate latitude lakes.

European lakes showing fish yields varying by taxa as a function of total phosphorus and water transparency. We scaled our curves to an easily measured productivity index in an attempt to increase their usefulness to managers. Other indices such as total phosphorus would also be suitable.

Discussion

Trophic continuum type models to predict fish yields exist in many forms. In focussing on the top predators of percid dominated lakes, we were able to obtain the largest possible and most reliable data set by using mean growing season [CHL] as the predictive variable.

We subjected data for a group of Canadian lakes and Lake Erie to regression anslysis. The objective was to see if a simple, easily understood, and precise estimator of walleye yield as a function of [CHL] could be obtained. Resulting regression lines indicated that a high proportion of variability in the yields of walleye and of total catch in this set of lakes could be explained by mean growing season [CHL]. A promising management tool for walleye-type lakes seemed well into development.

When additional data for highly productive lakes in Sweden were added, a new, more interesting picture emerged, one that defined *Stizostedion* yield in terms of a dome- or bell-shaped curve. We chose to define this as a band of yield values, which defined optimum range (approximately 7.5–12.5 mg $CHL \cdot m^{-3}$), maximum yield, and variability of yield over a wide range of [CHL], believing this to be the form of expressing our results of highest utility to fishery managers.

Even though such curves have been postulated by others (see above), this is the first instance we know of such a relationship being defined by a set of reliable data describing a group of lakes having similar fish communities. Since Fig. 2 represents a prototype, a closer analysis of its properties and some speculation on their significance is warranted. Elements of the curve we will discuss are its shape, width of the band defining this shape, and maximum and minimum yields.

The shape of the curve in Fig. 2 is essentially that of a normal distribution, indicating that its properties can be quantitatively analyzed using relatively simple, parametric statistics. The left-hand asymptote and ascending limb are presumably determined by a combination of interaction with more oligotrophic type fish communities and available food. If so, the former factor dominates at [CHL] < 5 mg $\cdot m^{-3}$. Between about 5 and 8 mg $\cdot m^{-3}$ flow of energy and material through food webs, as reflected by chlorophyll, would be increasingly important as yield determinants. The descending portion of the curve (>12 mg $\cdot m^{-3}$) reflects increasing competition with communities better able to use those types of food webs characteristic of more eutrophic conditions and/or habitat changes that become increasingly suboptimal for *Stizostedion*. Thus, although the two limbs are similarly configured, their shapes may be governed by different factors. Between [CHL] of 8 and 12 mg $\cdot m^{-3}$ the curve in Fig. 2 is relatively flat, indicating a broad range of lake trophic status that appears to be nearly optimal for *Stizostedion*.

The band we have drawn to define the yield – chlorophyll relationship has a consistent width of 2.5 kg $\cdot ha^{-1} \cdot yr^{-1}$. If this curve property is verified by further testing, it suggests that yields in the upper range of values might be predicted with an accuracy of about +15% and thus provide a valuable management tool. From the same perspective, the range of yield estimates <5 kg $\cdot ha^{-1} \cdot yr^{-1}$ would be of little use.

Minima and the maximum represent a universe of trophic states within which *Stizostedion* fisheries exist, and indicate ranges over which further field studies and experiments could be designed to profitably explore yield as a function of chlorophyll. Phosphorus loading–chlorophyll relationships are now well enough understood (Anonymous 1982b) so that lakes can, in many cases, be readily manipulated for [CHL]. Monitoring of *Stizostedion* population dynamics in such experimental systems would provide testing, refinement, and a further understanding of the relationship defined by Fig. 2. Competing communities (Fig. 3) could be introduced and managed in other experiments as an additonal variable.

Extant predictors, whether of the trophic type or others suggested at ASPY (Leach et al. 1987), give results in terms of total (all species) yield. This leaves fishery managers with the problem of apportioning yield between various stocks. In Fig. 2, slope of the line describing total fish yield is steeper than that for walleye alone, suggesting that as [CHL] increases, a proportionally larger part of the yield is from other taxa. This confirms the logic previously advanced by Hartmann (1977) and Colby et al. (1972) that stocks exist along a trophic continuum in aggregates with yields decreasing in a regular way on either side of optimum trophic state. We suggest that a standard objective for inland fishery science be to develop sets of curves (e.g. Fig.3) relating yield to trophic indices as a means of sorting out potential yields into appropriate stocks. To do so first requires a general knowledge of the game and/or commercial fish species in a lake or set of lakes. Johnson et al. (1977) described a system that provides a first-order approximation of this for Ontario lakes. Next, or in conjunction with the first step, information is needed on relative abundances as a function of whatever independent variable(s) is/are used as a total yield

estimator(s). Such a system of curves should only need to be constructed once for a given set of lakes unless major new stresses are imposed on the lakes. The relationship in Fig. 3, even though drawn largely from our own personal experience with some reference to Hartmann (1977) and Jones and Hoyer (1982), may be useful as a first approximation for lacustrine systems in the Great Lakes' basin.

Over much of the walleye range in North America, esocids complement and sometimes replace walleye as the dominant piscivore, thus producing a special problem in sorting out potential yields for these two stocks. We speculate that the walleye replacement by esocids is closely linked to the ratio of aquatic macrophytes to phytoplankton. So long as there is sufficient macrophyte-free area to support a true phytoplankton community, [CHL] may still suffice as an indicator of fish production. The proportioning of yield between percids and esocids needs to be evaluated by comparisons of lakes with varying levels of macrophyte occurrence. We suggest that percentage of a lake's macrophyte coverage × [CHL] in the macrophyte-free portion would be a useful index to test in this regard. Clearly, more research on this is required. We recommend strongly that future assessment of fisheries and lake environments include measurements of [CHL] and of the extent and nature of macrophyte beds so that relationships between these variables and potential fish yields can be developed

Given this caveat related to esocids, we are now able to modify our initial hypothesis to the following: "Yields of *Stizostedion* from lakes in which this is the dominant piscivore are related to average growing season chlorophyll concentration in the form of a dome-shaped curve over the range of 5–15 $mg \cdot chlorophyll \cdot m^{-3}$. At concentrations $<5\ mg \cdot m^{-3}$ and $>15\ mg \cdot m^{-3}$, factors other than lake trophic status, especially competition with fish in other taxonomic groupings, dominate yields."

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Multivariate Time Series Analysis of the Canadian Fisheries System in Lake Superior[1]

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Cohen, Y., and J. N. Stone. 1987. Multivariate time series analysis of the Canadian fisheries system in Lake Superior. Can. J. Fish. Aquat. Sci. 44 (Suppl. 2): 171–181.

Data for the Canadian fisheries system in Lake Superior were organized into monthly time series of catch and effort from January 1963 through December 1976 for six fish species. Multivariate, autoregressive (ARMA) models were identified for the system based on data for the first 140 mo. Forecasts were compared to data for the last 28 mo. The structure of the models indicate that (1) within the system, AR processes, as opposed to MA processes, were of overriding importance, (2) intraspecific interactions (inferred from data on catch-per-unit-effort, CPUE) were more prevalent than interspecific interactions, (3) interactions within the system occurred with lags of 1, 4, 12, 24, 25, 28, and 36 mo, (4) some of the trophic relationships among the fish species were revealed by the models, and (5) CPUE time series of lake trout (*Salvelinus namaycush*) affected, but was not affected by, the CPUE time series of other species. The models were used to forecast catch and CPUE for the last 28 mo, and the data were generally within one standard error of the forecasts. The models may help policy decision makers to explore the effects of inputs (e.g. quota regulations) and feedbacks within the fisheries' system on outputs (e.g. production, CPUE).

Les données concernant le système des pêches canadiennes dans le lac Supérieur ont été réparties en séries chronologiques mensuelles de prises et d'effort de pêche de janvier 1963 jusqu'à décembre 1976 inclusivement pour six espèces de poissons. On a établi pour le système des modèles autorégressifs à moyenne mobile (ARMM) et à plusieurs variables à partir de données recueillies au cours des 140 premiers mois. On a comparé les prévisions aux données pour les 28 derniers mois. La structure des modèles indique : (1) qu'à l'intérieur du système, les processus AR, par opposition aux processus à MM, avaient une importance prépondérante, (2) que les interactions intraspécifiques (déduites des données sur les prises par unité d'effort, PPUE) étaient plus répandues que les interactions interspécifiques, (3) que les interactions à l'intérieur du système se produisaient avec des décalages de 1, 4, 12, 24, 25, 28 et 36 mo, (4) que certaines des relations trophiques entre les espèces de poisson ont été révélées par les modèles et (5) que la série chronologique des PPUE de touladi (*Salvelinus namaycush*) concerné n'a pas été affectée par la série chronologique des PPUE d'autres espèces. Les modèles ont servi à prévoir les captures et les PPUE pour les 28 derniers mois et les données se situaient en général en deçà d'une erreur-type des prévisions. Les modèles peuvent aider ceux qui prennent des décisions politiques à examiner les effets des intrants (par ex. règlements sur les contingents) et les réactions à l'intérieur du système des pêches sur les extrants (par ex. production, PPUE).

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The problem of forecasting catch from fisheries systems is generally approached through mathematical or simulation models. These models are traditionally deductive, the so called mechanistic models (Beverton and Holt 1957; Schaefer 1957; Pella and Tomlinson 1969; Walters and Hilborn 1976; Deriso 1980; Schnute 1985), or inductive, the so called heuristic models (Mendelssohn 1980; Saila et al. 1980; Jensen 1985). Roff's (1983) simple autoregressive model falls between these two polarized approaches, and forecasts remarkably well.

Both the mechanistic and the heuristic approaches have common and unique advantages and shortcomings, which were lucidly reviewed by Poole (1978). Unless put in the context of the purpose for modeling, the question of which type of model is better is meaningless. This is particularly true if one views models as tools, rather than some sort of truism. On one hand, the heuristic approach is, for example, often superior for forecasting purposes to mechanistic models (Poole 1978; Roff 1983). On the other hand, simple systems, with few dynamics of overriding importance lend themselves to mechanistic modeling.

Multivariate time series analysis, an inductive approach, is recognized as a potentially powerful method for analyzing long sequences of time-related data from complex systems (Quenouille 1957; Hannan 1970; Akaike 1980). Such models aid in understanding dynamic relationships among system components. A better understanding of systems leads to improved

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control strategies and forecasts (compared with those based on data for a single component of the system). Due to computational difficulties and expense, applications of multivariate time series analysis have been, until recently, limited (Tiao and Box 1981). To our knowledge, multivariate time series analysis has never been applied to a fisheries system. The importance of the multivariate approach is further emphasized by the recent interest in multispecies-based fisheries management (Oglesby 1982; May et al. 1979; May 1984).

We applied multivariate time series models to catch–effort data for the Canadian fisheries system of Lake Superior. This data set is unique in being complete and detailed. The analysis revealed feedback relationships among the catch and effort of the various species. The results corroborated some of the biological facts known about the system, and reflected other patterns of interactions which could not be readily explained, but which undoubtedly existed.

The Data

All commercial fishers in Ontario have been required to complete a daily report of their catch (Hile 1962). The report includes date, location, species caught, weight by species, gear type, and effort (e.g. for gill nets, effort includes length of nets and depth). Each species caught, by date, constitutes an individual record in the data set, which in turn is organized into seven statistical districts (Smith et al. 1961). The data were obtained from the Fisheries Branch, Ontario Ministry of Natural Resources, Toronto, Ont.

We summarized the data from 1963 through 1976 by calendar month. Since most of the fishing effort and catch have been with gill nets, only gillnet catches were included. The data for all statistical districts were pooled to reflect the Canadian fisheries with gill nets from Lake Superior.

Multivariate Time Series Models

The central issues in multivariate time series analysis are (1) to identify the most parsimonious model, (2) use of the model for forecasting, and (3) use of the structure of the identified model to interpret the salient characteristics of the system.

Time series modeling can be considered as the building of a filter which reduces the data series to a white noise (random) process. The steps are (Box and Jenkins 1976) (1) transforming and differencing the data, if necessary, to make the series stationary and to remove seasonal effects, (2) calculating matrices of cross correlations and partial cross correlations with lags, (3) examining significant values in these matrices to identify the most parsimonious model in terms of number of parameters, (4) estimating parameters, (5) diagnostic checking, and (6) estimating the final parameters. Final parameter estimation is done by constraining the insignificant parameters (as identified from step 4) to zero. In addition, those parameters that are significant but make no biological sense are constrained to zero. Thus, some knowledge of the system reduces the number of parameters that need to be estimated, and enhances model identification. Step 5 consists of examining cross correlation matrices (with lags) of the residuals of the model fitted in step 4. Examination of the residuals determines whether the model fit in step 4 has reduced the data series to white noise. If not, the residuals may indicate a different model to fit. After step 6, step 5 is repeated to verify that the residuals remain uncorrelated over time. This procedure results in models with the fewest number of parameters (Tiao and Box 1981).

Multivariate time series models are represented by the relationships (Tiao and Box 1981)

$$(1) \quad \phi_p(B)z_t = \theta_q(B)a_t$$

where ϕ is a polynomial with matrix coefficients of degree p for the autoregressive (AR) parameters; B is a back shift operator, e.g. $B^2z_t = z_{t-2}$; z_t a vector (of dimension k) of the transformed time series; x_t, a vector of observations (e.g. CPUE, production, or effort) on k fish species at time t, $t = 1, 2, \ldots, n$, is transformed to z_t in order to make the series stationary and remove seasonal effects from the series; θ is a polynomial with matrix coefficients of degree q for the moving-average (MA) parameters; and a_t is a vector of k time series which have a multivariate normal distribution with mean zero and a constant covariance matrix over time. This matrix includes the statistical error (white noise). MA parameters are weighted on the white noise (versus the data series for AR parameters).

The Analysis

To explore system characteristics and to obtain production forecasts, we used two subsets of the data to identify two different multivariate time series models. The first subset was time series of catch-per-unit-effort (CPUE) for the six most consistently caught species or species groups: lake trout (*Salvelinus namaycush*), lake herring (*Coregonus artedii*), lake whitefish (*C. clupeaformis*), chubs species (*C. nigripinnis, C. zenithicus, C. reighardi,* and *C. hoyi*), walleye (*Stizostedion vitreum vitreum*), and yellow perch (*Perca flavescens*). The first four are the major commercial species in Lake Superior (MacCallum 1983), and the last two had been consistently caught during the period 1963–76. Our purpose of examining these time series was to investigate the extent of interspecific interactions, as revealed by the CPUE data, for the six groups of fish species and to relate the structure of the model to what is known about the fisheries' system in Lake Superior. We assume that CPUE reflects relative species'abundance (Gulland 1964; Peterman and Steer 1981; Bannerot and Austin 1983). This assumption obviously holds on an annual basis (e.g. December 1963, December 1964, ..., December 1976) but seasonally also reflects the catchability of the fish. For example, comparison of the CPUE for lake herring when they aggregate to spawn and the CPUE for midsummer when they are more dispersed tells little about the change in species' abundance, but the relative change can yield information for predictions (e.g. an increase in the CPUE between June of this year and last year may be useful information in predicting this December's CPUE). We assume that the data indirectly reflect the fisheries' system as a whole, including inputs such as fishers' behavior, market prices, regulations, and life history of the fish species.

The second subset of the data was time series of catch and effort data for lake trout, lake herring, and lake whitefish. These three were by far the most commonly caught species in Lake Superior (Baldwin et al. 1979). Our purpose was to investigate the interactions among the catches and efforts of these three species and to use the data to forecast catches.

The length of each of the time series was 168 mo (from January 1963 through December 1976). We used the first 140 observations for model identification and parameter estimation. To verify the two models, which were identified from the two

subsets of the data, we compared the remaining data with forecasts 28 mo in advance. The models were considered suitable reflections of the fisheries system if (1) the model reduced the data series to white noise and (2) the data were within one standard error of the forecasts.

Model identification, parameter estimation, and forecasting were computed by the SCA system for univariate–multivariate time series and general statistical analysis (Liu et al. 1983).

Model of six species' CPUE

Some of the series (Fig. 1) exhibited heterogeneity of the variance. We used the variance stabilizing transformation (Quinn 1985; Weisberg 1980)

$$(2) \quad y_{it} = \sqrt{1 + x_{it}}$$

where x_{it} is the CPUE at time t, = 1, 2, ..., 168 for species i, i = 1, 2, ..., 6. The fisheries system in Lake Superior is also highly seasonal (Fig. 1), with some series being nonstationary. Therefore, all the data were differenced according to

$$(3) \quad z_t = y_t - y_{t-12}$$

where z and y are vectors of dimension 6. This differencing removed the seasonal trends from the data and reduced the nonstationarity.

Following the above steps, the best model, in terms of uncorrelated residuals with lags, best fit, and forecasts closest to the data (Fig. 1), was

$$(4) \quad (I - \phi_1 B - \phi_4 B^4 - \phi_{12} B^{12})(I - \phi_{24} B^{24}) z_t = (I = \theta_1 B) a_t.$$

The modeling procedure therefore has reduced the lags to 7 (i.e. 1, 4, 12, 24, 25, 28, and 36) from the original 36 considered. The R^2 between the CPUE values derived from the model and those observed for the six time series were as follows: lake trout, 0.82; lake herring, 0.82; lake whitefish, 0.59; walleye, 0.73; yellow perch, 0.55; chubs, 0.68. The R^2 between the 28 forecasted values (i.e. the last 28 mo of the data which were not included in identifying model eq. 4) and the actual CPUE were as follows: lake trout, 0.73; lake herring, 0.81; lake whitefish, 0.87; walleye, 0.16; yellow perch, 0.59; chubs, 0.78.

The identified system (eq. (4), Table 1) indicates that the system was governed primarily by AR rather than MA processes. These pocesses operated with lags of up to the 3 yr considered. A cross correlation analysis of the series using annual data only did not reveal significant lags beyond 3 yr.

Most of the significant parameters were on the diagonal of the AR matrices θ (Table 1); therefore, most of the interactions within the system were primarily intraspecific. According to the model, the MA terms were lagged for 1 mo only, and then their effect disappeared. When the model was fitted without the MA matrix θ in Table 1, the fit (as indicated by the value of R^2) decreased only slightly. Still, the MA matrix was included, for without it the residuals became serially correlated.

To facilitate interpretation, we expanded eq. (4) (i.e. we multiplied the terms separated by parentheses) and considered lags within 4 mo as essentially operating during the same season. In other words, terms that included lags of say 24 and 28 mo were considered as operating at a lag of about 2 yr. Thus, we derived six simplified equations which qualitatively describe the system with lags of up to 3yr. These equations are summarized in Table 2 such that interactions among the CPUE for the species were represented by +, −, or zero, where + and − reflect positive or negative significant ($p < 0.05$) interactions.

TABLE 1. Structure of the six species' CPUE model (eq. (4)) showing the values of significant ($p < 0.05$) parameters. Insignificant parameters are indicated by 0. ϕ and θ denote matrices of autoregressive and moving-average parameters, respectively. LT, lake trout; LH, lake herring; WF, lake whitefish; WL, walleye; YP, yellow perch; CH, chubs species.

	LT	LH	WF	WL	YP	CH
			ϕ_1			
LT	0.34	0	0	0	0	0
LH	0	0	0	0	0.48	0
WF	0	−0.19	0	0	0	0
WL	0	0	0	0.26	0.21	−0.13
YP	0	0	0	0	0.46	0
CH	0	0	0	0.34	0	0.43
			ϕ_4			
LT	0	0	0	0	0	0
LH	0	0	0	0	0	−0.15
WF	0	0	0	0	0	0
WL	1.75	−0.30	0	0	0	−0.13
YP	0	0	0	0	0.17	0
CH	0	0	0	0	0	0.20
			ϕ_{12}			
LT	−0.38	0	0	0	0	0
LH	0	−0.28	0	0	0	−0.21
WF	0	0	−0.51	0	0	0
WL	0	0	0	−0.29	0	0.19
YP	0	0	0	0	−0.42	0
CH	0.77	0	0	0	0.29	−0.44
			ϕ_{24}			
LT	0	0	0	0	0	0
LH	0	−0.23	0	0	0.35	0
WF	0	0	−0.43	0	0	0
WL	0	0	0	−0.25	0	0
YP	0.83	0	0	0	0	0
CH	0	0.15	0	0	0	0
			θ_1			
LT	0	0	0	0	0	0
LH	0	0	0	0	0.49	0
WF	0	−0.25	−0.30	0	0	0
WL	0	0	0	0	0	0
YP	0	0	0	0	0	0
CH	0	0	0	0.44	0	0

For example, the row for lake trout in Table 2 indicates that its CPUE "led" itself during the same season (+ at lead 0 when lake trout is leading lake trout). In this case, the CPUE for lake trout for the present month would be high if the CPUE for the present season had been high, but if the CPUE 1 yr earlier had been high, the CPUE for the present month would be lower (− at lead 1 when lake trout is leading lake trout). Furthermore, no other species led lake trout (0 for all species leading lake trout).

Table 2 was used to construct Fig. 2. For example, consider lags for 1 yr (Fig. 2); species x is defined as leading species y if the parameter in column x row y of Table 2, under the column for lead 1, is significant. This parameter is derived from the appropriate AR matrix in eq. (4), after it was expanded. The value of the parameter can be either positive or negative (i.e.

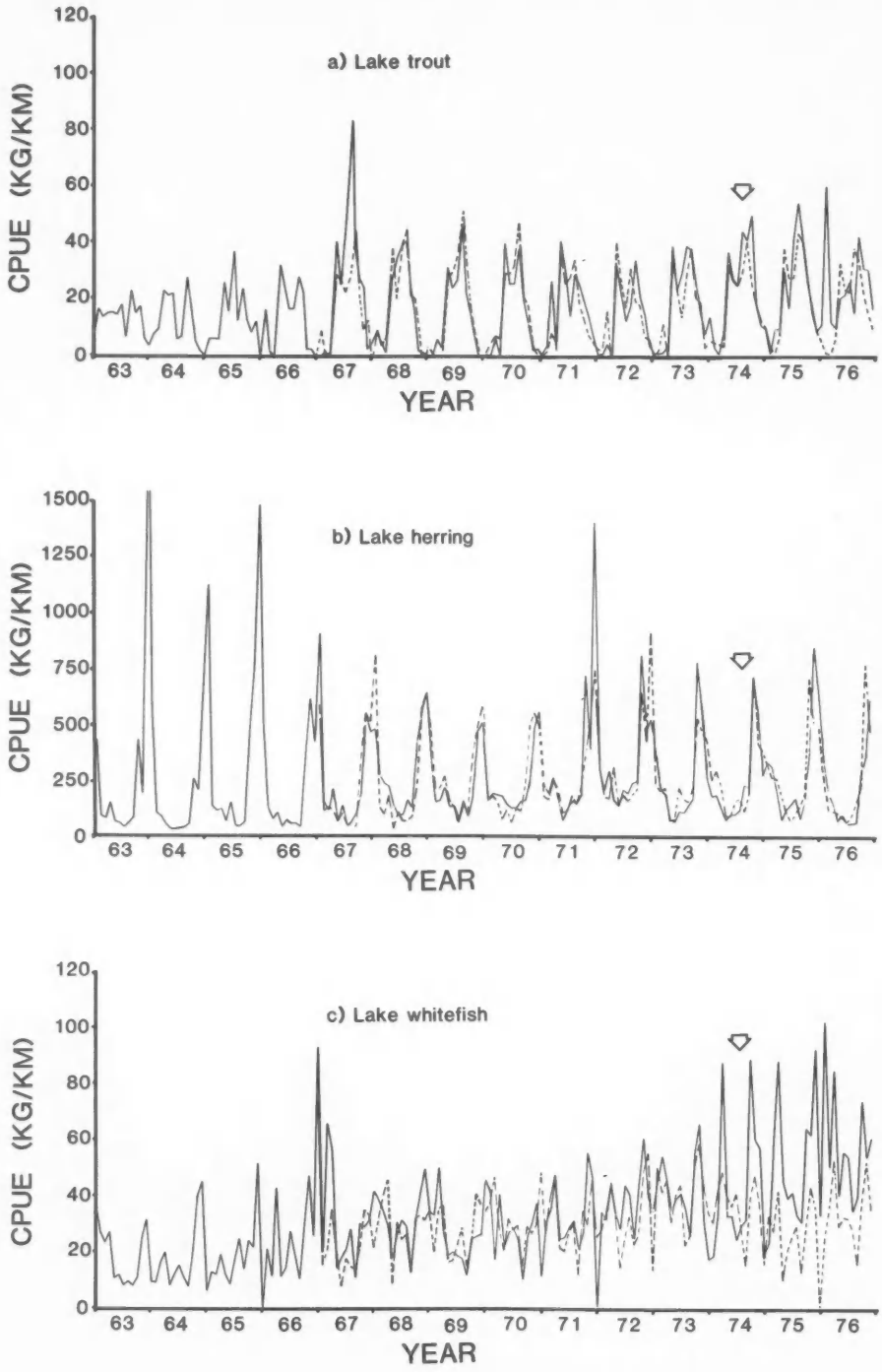

FIG. 1. Catch-per-unit-effort series (CPUE) (solid line) with model fit (broken line) and forecasts (beginning at the arrow) for six commonly caught species in Lake Superior. Data from arrow on were not used for model identification and fitting, and are shown for the purpose of comparison.

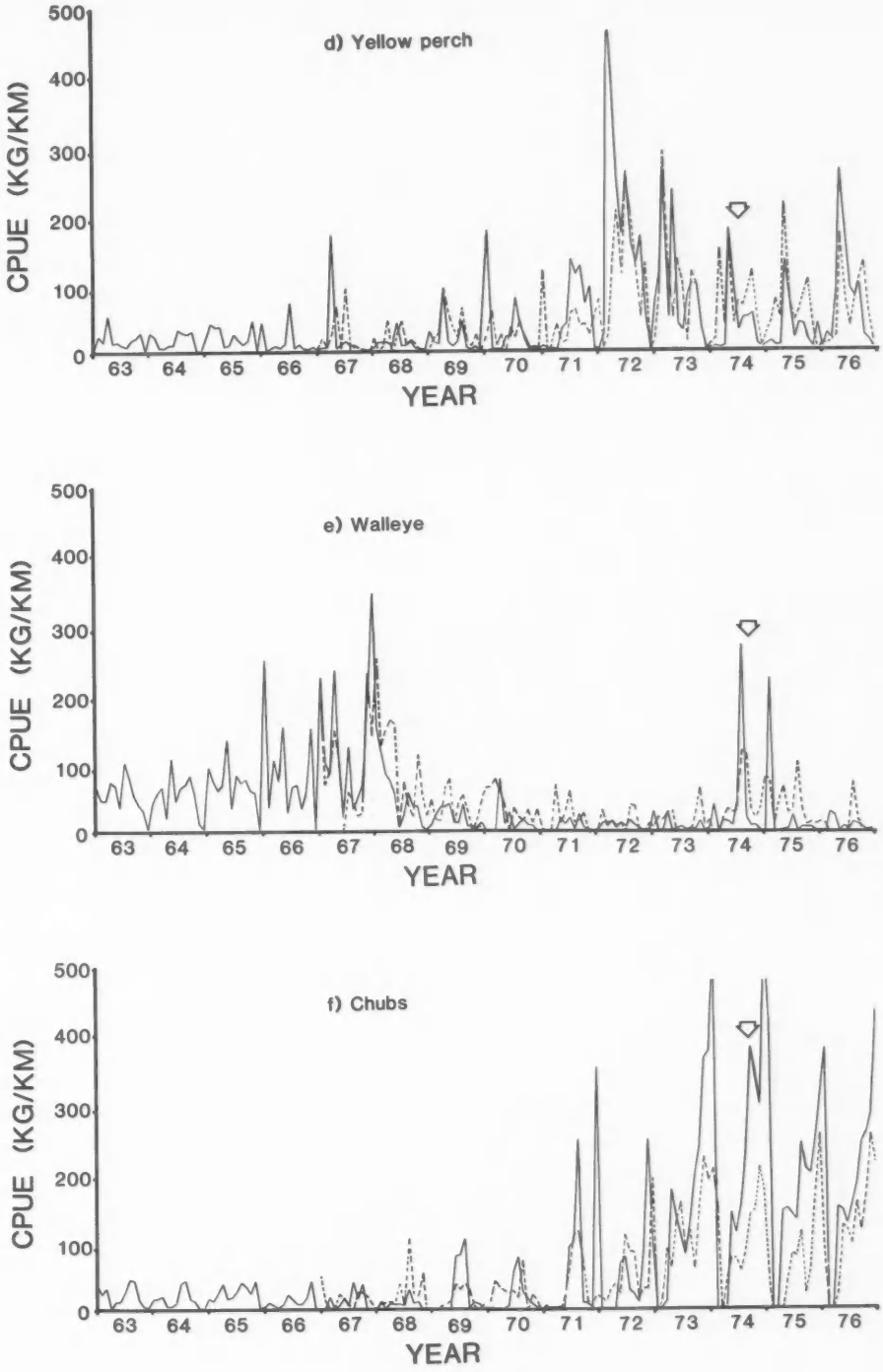

FIG. 1. (*Concluded*)

TABLE 2. Simplified interactions model for the Canadian fisheries system in Lake Superior, with the catch-per-unit-effort data for six common fish species: lake trout (LT), lake herring (LH), lake whitefish (WF), walleye (WL), yellow perch (YP), and chubs species (CH). The lead times are in years, and N denotes the effect of white noise, which includes no delays outside the same season.

	Leading species					
	LT	LH	WF	WL	YP	CH
Lead	0 1 2 3 N	0 1 2 3 N	0 1 2 3 N	0 1 2 3 N	0 1 2 3 N	0 1 2 3 N
LT	+ − 0 0 +	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0
LH	0 0 − 0 0	0 − − − +	0 0 0 0 0	0 0 0 0 0	+ 0 + + −	− − 0 0 0
WF	0 0 0 0 0	− 0 − 0 −	0 − − − +	0 0 0 0 0	0 0 + 0 0	0 0 0 0 0
WL	+ 0 − 0 0	− 0 − − 0	0 0 0 0 0	+ − − − +	+ 0 + 0 0	− + 0 0 0
YP	0 0 + + 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	+ − 0 0 +	0 0 0 0
CH	0 + 0 − 0	0 0 + + 0	0 0 0 0 0	+ 0 + 0 +	0 + 0 0 0	+ − 0 0 +

high catch of species x this year would correspond to low catch of species y next year if the parameter is negative). To avoid confusion, we present only the sign of the significant parameters in Table 2. If the parameter was not significant, a zero is indicated.

From Table 2 it is clear that all species lead themselves for 1-yr lags. Leading refers to the present value being significantly correlated with a past value. This is shown as a loop for the box of each species in Fig. 2. The sign of the lead is shown as well.

A simplified food web for Lake Superior (Fig. 3) was then compared with the web of interactions among the CPUE for the six species (Fig. 2). The arrows in Fig. 2 reflect interactions with lags; e.g. the arrow between the boxes for lake trout and lake herring indicates that CPUE for lake trout led CPUE for lake herring. Figure 2a represents the totality of interactions of CPUE with all lags of up to 3 yr, as revealed by the model (eq. 4). Since interactions change with lags (Table 2), "snapshots" of the interactions for the same season, and with lags of 1, 2, and 3 yr, were derived Fig. 2b, 2c, 2d, and 2e).

A comparison of Fig. 3 and Fig. 2a reveals certain similarities: lake whitefish is the most benthic feeder (Scott and Crossman 1973), and its unique position in the food web is also reflected by the model (Fig. 2a). It affected no other species, but was affected by lake herring and yellow perch, who feed in the more open waters (Scott and Crossman 1973).

Lake trout position in the web (Fig. 2a) is also unique. It is a piscivorous predator (Dryer et al. 1965; Martin 1966), but its CPUE was not affected by any of the other species. It did affect the CPUE of all other species on which it preys, except lake whitefish. This may be due to the regular stocking of lake trout which supports over 90% of the inshore fisheries (Lawrie and MacCallum 1980) and due to its wide prey base, including all six species (Scott and Crossman 1973). Goddard et al. (1987) found that fish community structure has little or no effect on actual yield of lake trout. Their conclusions are also consistent with those of Martin (1966) and Kerr and Martin (1970).

During the same season (Fig. 2b), the majority of interactions occurred between the feeders on herbivores (lake herring, yellow perch, and chubs; Fig. 3) and walleye, and all intraspecific feedbacks were positive. In other words, when CPUE were high, the fishers could expect the CPUE to remain high for the rest of the season. With 1-yr lag (Fig. 2c), lake whitefish was isolated; its CPUE was affected only by its own CPUE a year earlier, and overall, fewer interactions remained compared with within-season lags. Furthermore, the intraspecific interactions were negative for all species (Fig. 2c). With 2-yr lag, many more interactions were revealed (Fig. 2d), and with 3-yr lag (Fig. 2e), the interactions were fewer again. Except for within-season lags, all intraspecific interactions were negative and remained so for 3 yr. The signs of the lags cannot be clearly interpreted, for one cannot claim that a minus sign indicates competition; in fact, at times, even plus signs may reflect competition (Garsd 1984).

Figures 2a–2e may serve as a quick guide to managers, for they reveal some of the possible outcomes of perturbations to the system. For example, managers can expect no changes in future CPUE for lake trout if perturbations (such as stocking, harvesting, etc.) no larger than those that had occurred between 1963 and 1976 were to occur in the future. Thus, as long as the CPUE of other species do not fluctuate more than past fluctuations, the CPUE of lake trout in the future should not be affected.

Not all apparent interactions (Fig. 2a) can be explained in terms of the biology of the species. The model encapsulates data which reflect all inputs to the system, including fishers' behavior, market prices, the kinds of gear that are used to catch the various species, conditions in the breeding sites, changes in abundance of other species (e.g. sea lamprey (*Petromyzon marinus*)), controls, and quota regulations (e.g. on lake trout). Furthermore, some of the parameters which indicate interactions may be spurious due to the large number of parameters which were estimated. Nine spurious correlations may be expected for the 180 parameters estimated at the 5% significance level. However, we fitted models with different lags; in most cases, the position of significant parameters in the structural matrices (Table 1) did not change.

Model of Production and Effort of Three Species

The data were first transformed to reduce the variance according to

$$(5) \quad y_t = \ln x_t$$

where x_t is either the catch or effort for these three species and ln is the natural logarithm. The vectors y_t were then differenced according to (3).

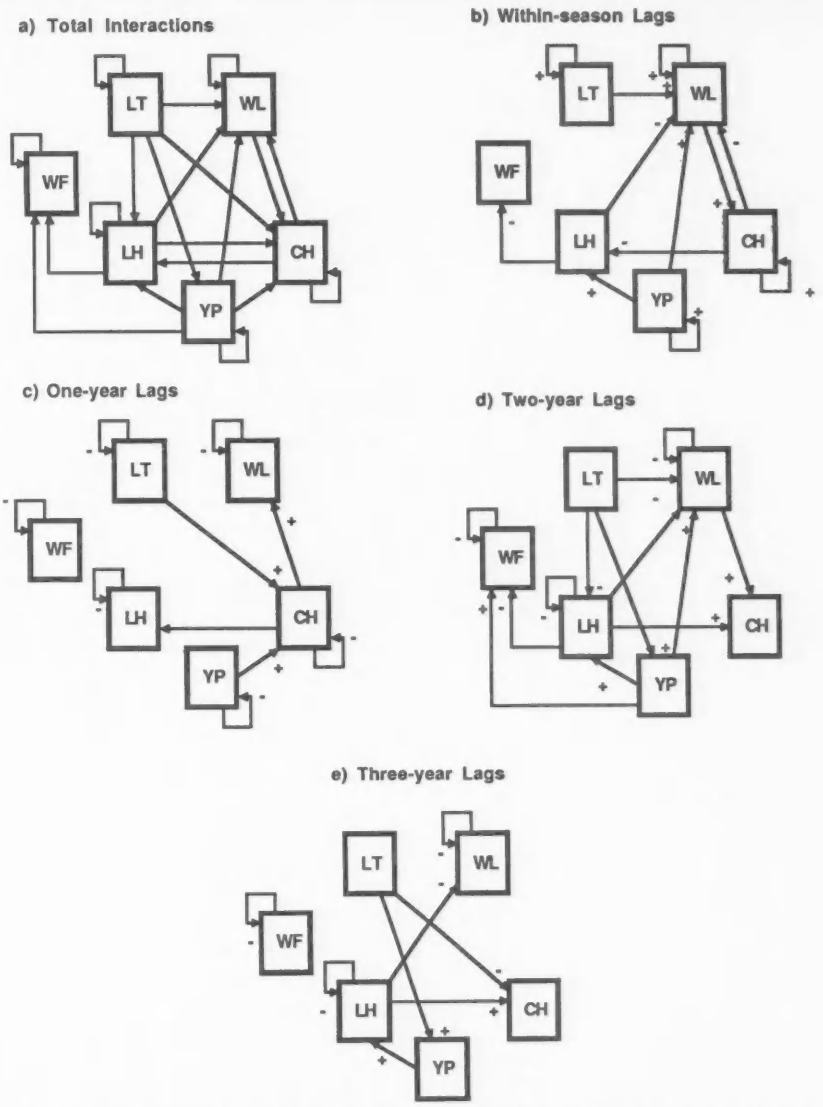

FIG. 2. Simplified web of interactions of CPUE for six commonly caught species in Lake Superior according to eq. (4). Arrows indicate that the CPUE for the species at the tail of the arrow is leading; + indicate positive interactions (i.e. high CPUE leads high CPUE); − indicate negative interactions. LT, lake trout; LH, lake herring; WF, lake whitefish; WL, walleye; YP, yellow perch; CH, chub species.

The model with best fit, and with uncorrelated residuals was identified as

$$(6)\quad (I - \phi_1 B - \phi_6 B^6)(I - \phi_{12} B^{12}) z_t = (I - \theta_1 B) a_t.$$

As in eq. (4), the model indicates a predominantly AR process, but with different lags. Twelve-month lags were identified even after the seasonal effect was removed from the series. Following the procedure for the model for six species, we expanded the equations (Table 3) and plotted snapshots of the interactions for the lags (Fig. 4).

No lags greater than 2 yr operated in the system (eq. (6)), and the majority of feedbacks were intraspecific (Table 3) and negative (Fig. 4). The time series of catches of lake trout was independent of any other species, and was essentially a univariate series (Fig. 4a) of the form

$$(7)\quad z_1(t) = -0.417 z_1(t - 12) + a_1(t)$$

where $z_1(t)$ is the ln-transformed and differenced catch series for lake trout and $a_1(t)$ are normally distributed and uncorrelated random shocks with mean zero and standard deviation of 0.063. This, again, may be a result of the regular stocking and regulation of lake trout. The effort series for lake trout had no feedback from any other series, and led the efforts (but not

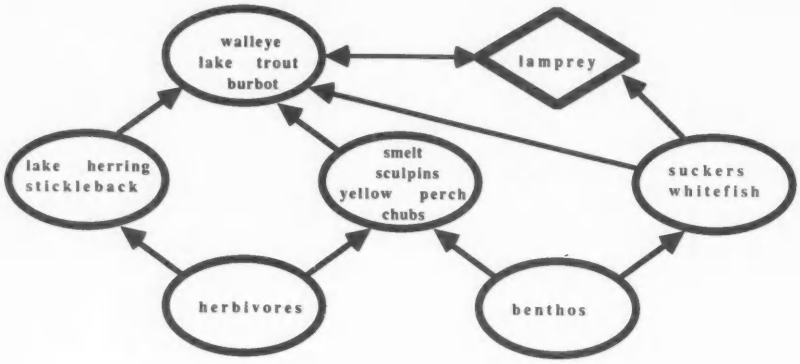

FIG. 3. Simplified food web for Lake Superior. Adapted from Jones (1982).

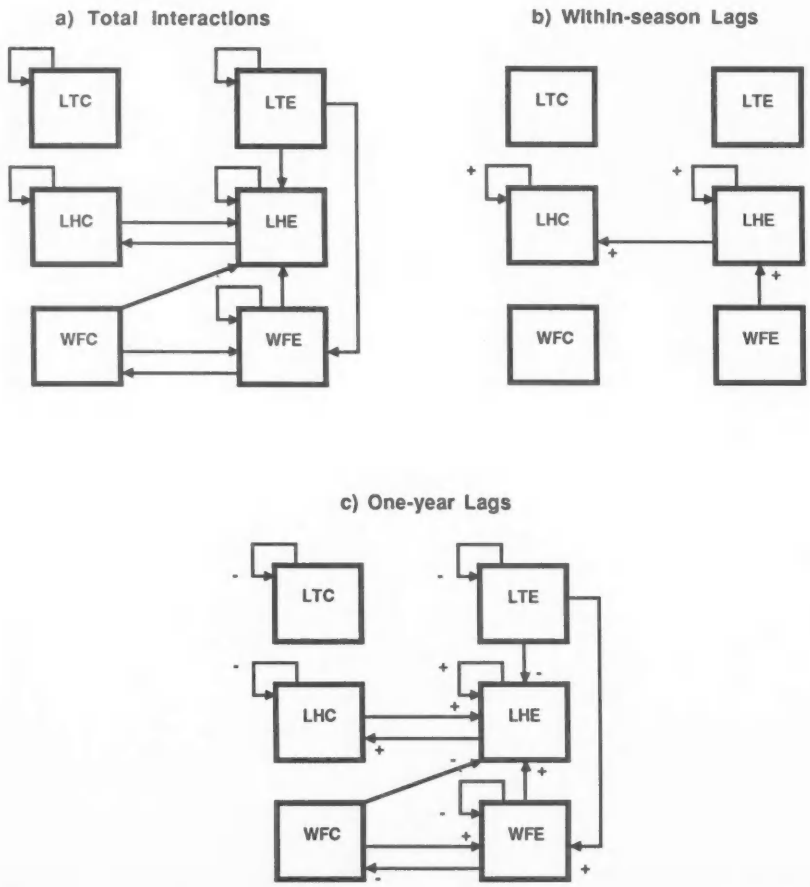

FIG. 4. Simplified web of interactions of catches and efforts for three commonly caught species in Lake Superior according to eq. (6). Arrows indicate that the variable shown in the box at the tail of the arrow is leading; + indicate positive interactions (i.e. high CPUE leads high CPUE); − indicate negative interactions. LTC, lake trout catch; LTE, lake trout effort; LHC, lake herring catch; LHE, lake herring effort; WFC, lake whitefish catch; WFE, lake whitefish effort.

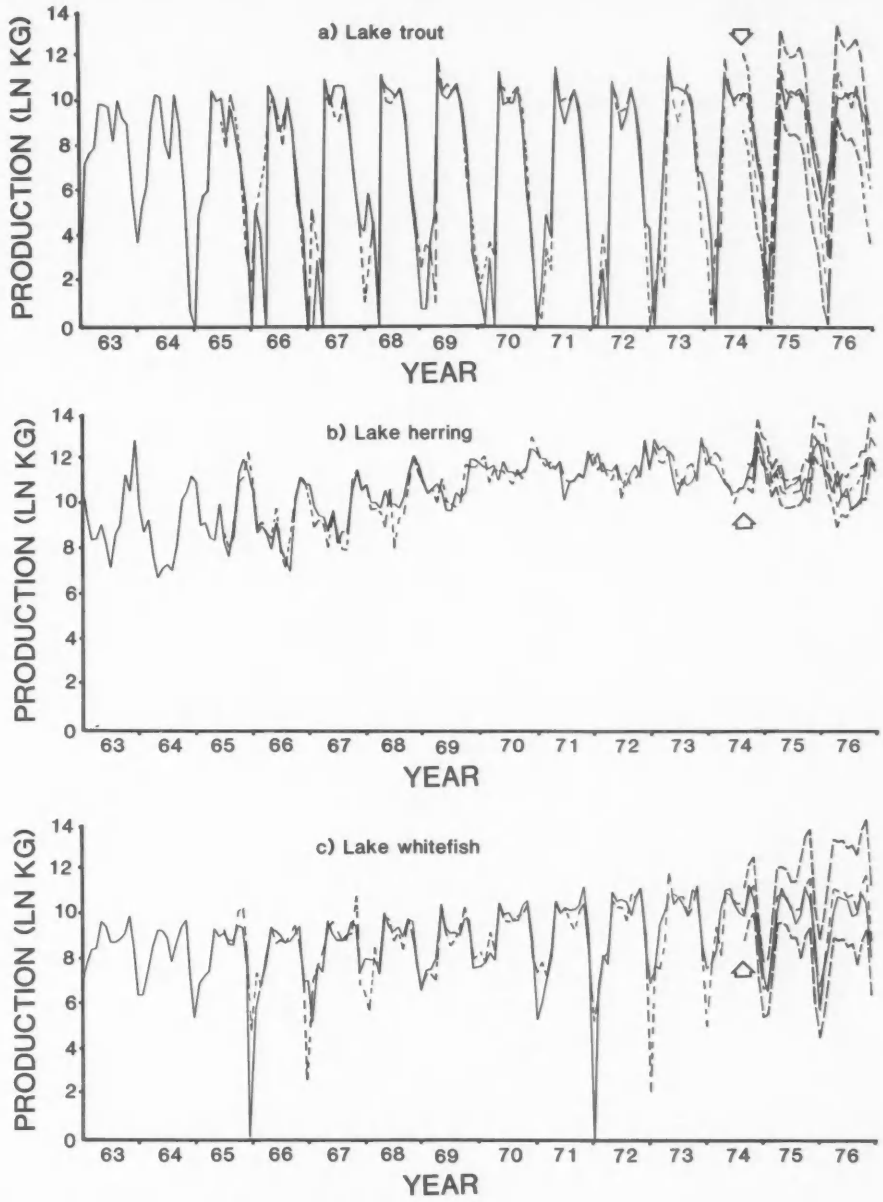

FIG. 5. Catch series (solid line) with model fit (broken line) and forecasts (beginning at the arrow) with their one standard error (upper and lower broken lines) for three commonly caught species in Lake Superior. Data from the arrow on were not used for model identification and fitting, and are shown for the purpose of comparison. Efforts were considered nonforecastable.

catches) for lake herring and lake whitefish (Fig. 4a). Overall, there were no feedback relationships among the catches, while there were among efforts (Fig. 4a).

The two series for lake herring displayed feedback relationships (Fig. 4a) where during the same fishing season, high effort resulted in high catch, with the reverse not being true (Fig. 4b). High catch in one year resulted in high effort a year later, and high effort in one year resulted in high catch a year later (Fig. 4c). Such relationships may be a reflection of long lags in feedbacks, and hence unstable fisheries (Selgeby 1982). Because of the sequential overexploitation of discrete unit stocks (Selgeby 1982), once low catches or low efforts occurred, they tended to persist.

For lake whitefish (Fig. 4b and 4c) the case was slightly

TABLE 3. Simplified interactions model for the Canadian fisheries system in Lake Superior, with the catch (C) and effort (E) data for lake trout (LT), lake herring (LH), and lake whitefish (WF). The lead times are in years, and N denotes the effect of white noise, which includes no delays outside the same season.

	Leading species					
	LTC	LHC	WFC	LTE	LHE	WFE
Lead	0 1 N	0 1 N	0 1 N	0 1 N	0 1 N	0 1 N
LTC	0 − +	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0
LHC	0 0 0	+ − +	0 0 0	0 0 0	+ + 0	0 0 0
WFC	0 0 0	0 0 0	0 0 +	0 0 0	0 0 0	0 − 0
LTE	0 0 0	0 0 0	0 0 0	0 − +	0 0 0	0 0 0
LHE	0 0 0	0 + 0	0 − 0	0 − 0	+ − +	+ + 0
WFE	0 0 0	0 0 0	0 + 0	0 + 0	0 0 0	0 − +

TABLE 4. Coefficient of determination (R^2) for the forecast against actual productions of eq. (6) for forecasts up to 6, 12, and 28 mo.

	R^2		
	6 mo	12 mo	28 mo
Lake trout	0.86	0.85	0.77
Lake herring	0.91	0.88	0.79
Lake whitefish	0.83	0.84	0.78

different. High effort one year resulted in low catch next year, and high catch one year resulted in high effort next year. This result reflects an intuitively clear behavior of fishers, and is also a reflection of stable fisheries (Fig. 1).

Compared with the system identified for the six species' CPUE, the system of only three species is closer to a random walk process (lags operated for up to 1 yr only). The model of production and effort of the three species also reflects fishers' behavior and may be used in reference to decision making. For example, one might expect that higher efforts on lake trout would not necessarily result in higher efforts for lake whitefish and lower efforts for lake herring (Fig. 4a). Incidental catches of lake whitefish, though, are found in lake trout nets and vice versa (MacCallum 1983), but lake herring are less likely to be caught in these larger mesh sizes.

For forecasting purposes, we considered efforts as inputs to the system (they were not forecast), and used the model (eq. (6)) to forecast production for 28 mo in advance. The forecasts were reasonable (Table 4; Fig. 5) and the model can certainly be used for forecasting purposes. As expected, forecasts closer to the start of the forecasts are better (Table 4). The farther the forecast is from the start, the more reliance on previous forecasts is needed. We are assuming that future perturbations to the system would not be larger than those that occurred during the period for which the data arose.

Conclusions

Both models indicate that compared with interspecific interactions, intraspecific interactions were ubiquitous. Single-species models for lake trout were justifiable on the basis of this data set. For other species, however (e.g. lake herring), they were not (Fig. 2a and 4a). The models allowed separation of input and feedback relationships within the system. For example, there were feedback relationships between the CPUE series for lake herring and chubs, whereas the CPUE for lake trout can be viewed as input to the CPUE series of lake herring. Other relationships are detailed in Fig. 2 and 4.

Both models reflected, to some extent, biological relationships among the species (e.g. lake trout predation on lake herring). The models also encapsulate fishers' behavior (e.g. the instability of lake herring fisheries), and do not rely on a priori assumption of system characteristics. An assumption that we do make is that the fish species used are likely from the same system (i.e. Lake Superior commercial fishery). Large forecast errors may occur due to spurious correlations if no direct relationship is present between the time series, and if new perturbations which did not occur in the past appear. The models may also serve as guidelines for decision makers.

Our approach is clearly inductive, but multivariate time series analysis can also be deductive. One can make a priori assumptions about the system and structure part of the model accordingly. For example, the forecasts of the model of production and effort of the three species were calculated with efforts which could not be forecast. When other mechanisms are known, the system may be partially modeled by forcing some of the parameters in the preliminary identification stage to be zero. For instance, if the effect of weather is to be included, one can hardly expect fish abundance to affect weather, and the transfer coefficients between fish and weather in the model should be set to zero. As such, multivariate ARMA models can certainly be both deductive and inductive and a tool useful in fisheries management.

As additional data become available, we hope to include data prior to 1963 and after 1976 to obtain parameters that encompass a wider set of perturbations (i.e. pre- and post-lamprey control).

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Changes in the Multispecies, Winter Angling Fishery of Lake Simcoe, Ontario, 1961–83: Invasion by Rainbow Smelt, *Osmerus mordax*, and the Roles of Intra- and Interspecific Interactions[1]

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Evans, D. O., and P. Waring. 1987. Changes in the multispecies, winter angling fishery of Lake Simcoe, Ontario, 1961–83: invasion by rainbow smelt, *Osmerus mordax*, and the roles of intra- and interspecific interactions. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 182–197.

Winter creel surveys revealed major changes in the abundance of five fish species (lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus clupeaformis*, lake herring, *Coregonus artedii*, yellow perch, *Perca flavescens*, and rainbow smelt, *Osmerus mordax*) in Lake Simcoe (1961–83). Variations in abundance were in part caused by intra- and interspecific factors. Catches in alternate years for both lake herring and rainbow smelt were inversely correlated, suggesting negative interactions between their young-of-the-year and yearlings. Similarly an inverse relation between parental stock size and recruitment explained a significant component of the catch variation of lake herring and yellow perch. Natural recruitment of lake trout declined during the 1950s (associated with eutrophication effects), and in the early 1960s, rainbow smelt invaded the lake. Lake whitefish abundance declined in the early 1970s as smelt abundance increased; the decline in whitefish recruitment was probably caused by interaction between smelt and whitefish young-of-the-year. Catches of yellow perch were positively correlated with rainbow smelt and negatively correlated with lake whitefish. Lake herring also increased when lake whitefish density was low. Increased abundance of lake trout after 1975 (due to stocking) appears to have resulted in lower densities of lake herring, rainbow smelt, and yellow perch and the reestablishment of lake whitefish recruitment at a low level. These results suggest that a large predator (lake trout) can have a major influence on the structure of a fish community, by direct and indirect effects.

Des enquêtes sur la pêche sportive en hiver ont révélé des variations importantes de l'abondance de cinq espèces de poisson (le touladi, *Salvelinus namaycush*; le grand corégone, *Coregonus clupeaformis*; le cisco de lac, *Coregonus artedii*; la perchaude, *Perca flavescens* et l'éperlan arc-en-ciel, *Osmerus mordax*) peuplant le lac Simcoe (1961–1983). Les variations de l'abondance étaient en partie dues à des facteurs intra et interspécifiques. Une année sur deux, les prises de cisco de lac et d'éperlan arc-en-ciel étaient en corrélation inverse ce qui porte à croire à des interactions négatives entre leurs jeunes d'un an et moins. De même, une relation inverse entre la taille du stock parental et le recrutement explique dans une large mesure la variation des prises de cisco de lac et de perchaude. Le recrutement naturel du touladi a diminué au cours des années 1950 (associé à l'eutrophisation), et au début des années 1960, l'éperlan arc-en-ciel a envahi le lac. La baisse du nombre de grands corégones au début des années 1970 a été accompagnée d'une augmentation de l'abondance de l'éperlan arc-en-ciel; la chute du recrutement du grand corégone a probablement été causée par une interaction entre les éperlans et les corégones de moins d'un an. Les prises de perchaude étaient en corrélation positive avec celles d'éperlan arc-en-ciel et en corrélation négative avec celles de grand corégone. Le nombre de ciscos de lac a aussi augmenté en fonction d'une faible densité de grand corégone. Une plus forte abondance de touladi après 1975 (suite à des ensemencements) semble avoir entraîné de plus faibles densités de cisco de lac, d'éperlan arc-en-ciel et de perchaude et le rétablissement du recrutement du grand corégone à un faible niveau. On peut interpréter ces résultats en disant qu'un gros prédateur (le touladi) peut avoir, directement et indirectement, une grande influence sur la structure d'une communauté de poissons.

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An annual creel survey of the winter angling fishery on Lake Simcoe has been conducted by the Ontario Ministry of Natural Resources since 1961. The primary objectives of the survey are to determine the level of fishing effort and to monitor fluctuations in the catches of five major species (lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus clupeaformis*, lake herring, *Coregonus artedii*, yellow perch, *Perca flavescens*, and rainbow smelt, *Osmerus mordax*). The resulting data are used by local managers to regulate the fishery. These data also provide a basis for investigating the underlying ecological processes that influence species abundances. This paper is primarily concerned with the effects of species interactions, both intra- and interspecific, on variation in species abundances in the fish community.

The fishery takes place from January to March, provides an average of 443 000 angler-hours of fishing each year, and harvests 80 000 to 100 000 kg of fish annually. In recent years, however, changes have occurred in the species composition of the catch (DesJardine and Lawrence 1979; Willox 1985). Rainbow smelt were introduced from an unknown source about 1960 (MacCrimmon et al. 1983) and subsequently have become abundant in the lake. Also, recruitment failure has occurred in lake trout and lake whitefish during the years of the survey (DesJardine and Lawrence 1977; Evans 1978; Evans et al. 1986), and catches of yellow perch have increased. We have used the creel survey data to evaluate the involvement of species interactions in these changes.

The main objectives of the study are to describe variations in the annual catches and relative abundances of the major species in the winter fishery and to determine whether variation in the relative abundances of the major species can be attributed mostly to either intra- or interspecific factors. Of particular interest is the possible effect of rainbow smelt on the abundance of other species. However, all possible interactions among the major species are considered.

Time series analysis (Nelson 1973) and correlation methods are used to describe and compare catch variations within and between species. Three major hypotheses are tested: (1) changes in the yields of all species in the winter fishery are a direct result of the introduction of rainbow smelt; (2) *intra*specific interactions explain a significant amount of the variability in the yields of individual species; and (3) *inter*specific interactions explain a significant amount of the variability in the yields of individual species. Intraspecific factors refer to density-dependent interactions between cohorts or between the adult stock and the new recruits, either age 0 or entrants to the fishery. Interspecific factors include negative (predation, competition) and positive (mutualism, commensalism) effects.

Methods

Study Location

Lake Simcoe is the fifth largest of Ontario's inland lakes (surface area 725 km^2). The lake, located in south-central Ontario is relatively shallow (mean and maximum depths of 17 and 41 m, respectively) and has a regular shoreline, with two large bays, Cook Bay, which is shallow and eutrophic (maximum depth 15 m), and Kempenfelt Bay, which is deep (maximum depth 41 m) and mesotrophic (Fig. 1). The central basin of Lake Simcoe is mesotrophic; Secchi disk varies from 2.5 to 5.0 m during summer (Ralston et al. 1975). The lake is dimictic and dissolved oxygen levels within 1–2 m of bottom in the hypolimnion often decline to ≤ 1 $mg \cdot L^{-1}$ during late summer (Evans 1978). The water is alkaline (pH 8.3, alkalinity 125 $mg \cdot L^{-1}$) and has high total dissolved solids (208 $mg \cdot L^{-1}$).

Source of Data

Data analyses in this paper are based on creel surveys conducted from 1961 to 1983. Surveys were not conducted in 1962, 1969, or 1980. The creel survey is a roving type (Malvestuto 1983; Malvestuto et al. 1978) in which the surveyors contact anglers during their fishing trip and determine the number of hours of fishing effort, the numbers of each species of fish captured, and other socio-economic information (Willox 1985). The duration of safe conditions for angling on the ice has varied from 45 d in 1973 to 80 d in 1978, the mean being 70 d. The creel survey normally spans the entire safe-ice period and has provided observations on 55–90% of the days. In 1977, a shortened season was introduced for lake trout and lake whitefish, ending on March 15 (approximately 60-d season) regardless of ice conditions. Catches for these species, since 1977, have been extrapolated to 70 d for comparison with earlier years; hence, their yields reported here are about 14% larger than the actual estimated landed catch for the period 1977–83.

Statistical Analyses

To obtain estimates of the relative abundances of species over years, total catches were adjusted to a 70-d season (mean length of all seasons) and to the mean annual angling effort (442, 925 $h \cdot yr^{-1}$). Catchability of angling gear for each species was assumed to remain constant during the survey period. Catchability is suspected to vary between species, but this does not seriously affect interspecific correlations of relative catches over time.

Trends and residuals in the catch series for each species were separated out using a compound smoothing technique (3 RSSH, twice, Velleman and Hoaglin 1981). The residuals are the deviations of the catch data from the trend lines. The absolute size of the irregular component depends upon the size of the catch. To indicate the relative amount of variation in abundance between species, the residuals are shown as percentages of the trend.

Autocorrelation coefficients (ACR) were calculated for the effort-corrected, unsmoothed catch series for each species in order to test for randomness in the residuals. Significant autocorrelation indicates that successive residuals are correlated and, hence, not independent of one another. Significant autocorrelation was found in the catch series of each species, and therefore, we applied Bartlett's formula to adjust the number of degrees of freedom as follows:

$$n^* = \frac{n}{\left[\frac{1 + (r_{a1})(r_{a2})}{1 - (r_{a1})(r_{a2})}\right]}$$

where n^* is the number of independent observations, n is the number of real observations, and r_{a1} and r_{a2} are the first-order autocorrelation coefficients, respectively, for the two catch series being tested (Ezekiel and Fox 1959). The adjusted number of degrees of freedom (i.e. $n^* - 2$) is used to test the statistical significance of correlation coefficients between two catch series.

We employed partial autocorrelation (PACR) analyses of

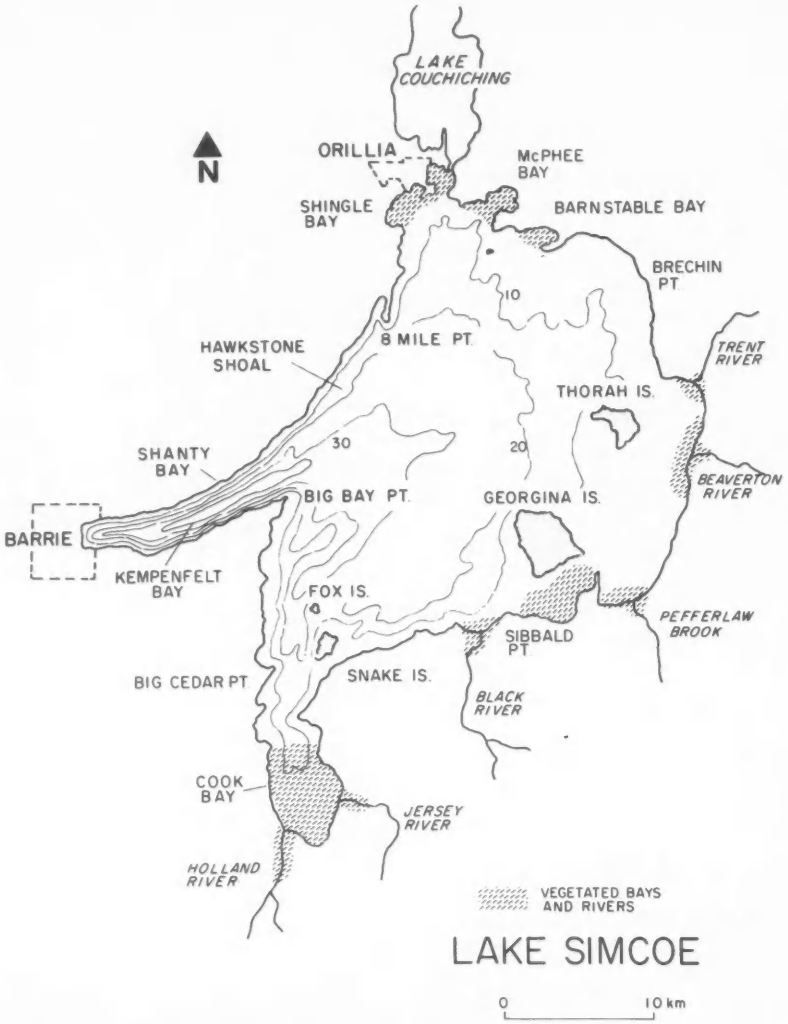

FIG. 1. Lake Simcoe showing depth contours at 10-m intervals and geographic locations referred to in the text.

first differences of the catches for the five major species to test the intraspecific interaction hypothesis. PACR coefficients were calculated for each of the untransformed catch series and their first differences at lags from 2 to 10 yr. PACR removes the effect of correlations between adjacent residuals being transferred along the series at lags exceeding 1 yr and allows a test of density-dependent intraspecific effects of one adult population on subsequent ones. First differencing removes autocorrelation while retaining the temporal patterns in the data (Ezekiel and Fox 1959, p. 340–342). The square of the partial correlation coefficient at a lag equivalent to the generation time of the population corresponds to the amount of variability transferred from one generation to the next (Garsd 1984). We employed the PACR analyses of first differences to test the intraspecific interaction hypothesis (hypothesis 2).

The interspecific hypothesis (hypothesis 3) was evaluated using pairwise correlation analyses of the catch series for each possible species pair. For each of the 10 interspecific pairwise comparisons, lag times of ±0–8 yr were tested (i.e. correlations between the catch series of one species beginning at t_0, t_1,…,t_8 were compared with the catches of the other beginning at t_0, and vice versa). The lagged comparisons allow testing of a subset of hypotheses, within hypothesis 3, that address specific types of interspecific interactions. The subhypotheses of most interest are as follows: (1) interaction occurs between the adults of two species (competition or predation); (2) interaction occurs between the young-of-the-year of one species and the adults of another (predation); (3) interaction occurs between the young-of-the-year of two species (competition, predation); (4) interaction occurs between the yearlings of one species and the young-of-the-year of another (competition, predation); and (5) interaction occurs between the adults of one species and the eggs of another (predation).

Knowledge of the mean ages of the fish in the catches is

TABLE 1. Summary of fish harvest in numbers (1000s), kilograms (1000s), and kilograms per hectare for the winter angling fishery on Lake Simcoe from 1961 to 1983. All values are adjusted to correspond to a 70-d fishing season.

Years	Effort (1000s h) (mean ± SD)	Statistic	Species					Total
			Lake trout	Lake whitefish	Lake herring	Yellow perch	Rainbow smelt	
1961–65	411.3±96.5	Mean catch ± SD	2.7±1.0	125.2±67.4	68.0±39.2	35.0±19.3	0.13±0.15	231.0
		kg	9.7	53.6	19.7	5.2	<0.01	88.2
		kg·ha^{-1}	0.13	0.74	0.27	0.07	<0.001	1.22
1966–68	390.8±66.5	Mean catch ± SD	1.5±0.8	136.7±23.6	55.6±19.4	32.1±3.5	2.9±2.9	228.8
		kg	5.6	74.2	16.1	4.8	0.1	100.8
		kg·ha^{-1}	0.08	1.02	0.22	0.07	0.004	1.39
1970–72	431.4±58.6	Mean catch ± SD	1.3±0.6	57.7±15.1	70.0±19.5	122.3±62.0	109.3±51.8	360.6
		kg	5.6	45.3	20.3	18.3	3.3	92.8
		kg·ha^{-1}	0.08	0.62	0.28	0.25	0.05	1.28
1973–75	416.2±10.6	Mean catch ± SD	0.9±0.2	23.3±15.5	81.7±53.1	213.5±56.6	129.2±86.2	448.6
		kg	3.1	21.9	23.7	32.0	3.9	84.5
		kg·ha^{-1}	0.04	0.30	0.33	0.44	0.05	1.17
1976–79	502.0±80.2	Mean catch ± SD	6.5±0.9	6.8±3.1	191.6±90.7	237.4±81.1	92.8±44.0	535.1
		kg	15.6	8.4	55.6	35.6	2.8	117.9
		kg·ha^{-1}	0.21	0.12	0.77	0.50	0.04	1.63
1981–83	496.7±46.6	Mean catch ± SD	7.1±2.7	17.2±0.9	68.0±0.5	173.8±63.2	109.6±36.7	352.9
		kg	16.0	23.1	19.7	26.1	3.3	88.2
		kg·ha^{-1}	0.22	0.32	0.27	0.36	0.05	1.22

required to test the subhypotheses. For example, if the mean age of recruitment of lake whitefish and rainbow smelt in the winter catch is 7 and 3 yr, respectively, interaction between their young-of-the-year, affecting the survival of one member of the pair, would occur with a 4-yr lag (smelt leading) between the catches.

Results

Trends and Variations in the Catch

Anglers catch primarily five species: lake trout, lake whitefish, lake herring, yellow perch, and rainbow smelt (Table 1). Northern pike, *Esox lucius*, walleye, *Stizostedion vitreum vitreum*, common white sucker, *Catostomus commersoni*, and burbot, *Lota lota*, are also caught, but infrequently. Since 1961, when the creel survey was initiated, catches of the major species have fluctuated widely (Fig. 2 and 3). The total number of fish caught per 70-d season each year has increased (Fig. 2; Table 1), but the total biomass caught per year has remained at about the same level (Fig. 3; Table 1). The catch trends are modified significantly, however, after correction to the mean annual fishing effort. Total relative catch (corrected for effort) increased in 1971, remained high during the mid-1970s, and declined during the late 1970s (Fig. 4). The effort-corrected catches provide a better approximation of the relative abundance of each species. Annual variation in the relative catches of each species, when separated into their trend and irregular components, indicates marked instability during the study period (Fig. 5 and 6). Catches of individual species revealed either marked upward or downward trends or both, coefficients of variation ranging from a low of 58% for lake herring to 98.5% for rainbow smelt, and the trend component explaining 61.4% (smelt) to 93.2% (lake whitefish) of the total variation (Table 2).

Lake Trout

Lake trout abundance declined during the 1960s, reached a minimum during the early 1970s, and increased steeply during the late 1970s (Fig. 5). The decline in the 1960s is a result of reproductive failure during the 1950s, very few young, non-hatchery trout being seen during the later period (DesJardins and Lawrence 1979). Increase in numbers of trout during the late 1970s is due primarily to increased planting of hatchery-reared yearlings, beginning in 1973 (Fig. 7). A linear least-squares fit of the relationship between the number of trout planted and the catch 4 yr later explains about 52% of the variation in the annual catch. On average, the maximum catch for hatchery yearlings occurred 4 yr after planting. Figure 7 suggests a density-dependent relationship in which the catch increases as a function of the number planted up to about 8×10^4 yearlings, but then declines at higher stocking densities.

Variability of lake trout catches about the trend is relatively low, with the exception of a major deviation in 1976–77 (Fig. 6) caused by an abrupt increase in catch which corresponds to increased stocking. Two distinctive periods, therefore, characterize the lake trout catch series: the pre-1975 decline and the post-1975 recovery (Fig. 4 and 5). Catches during both periods are confounded by the presence of hatchery fish. The possible effects of species interactions on natural reproduction and recruitment of lake trout, therefore, cannot be determined on the basis of the present data.

Lake Whitefish

Catches of lake whitefish declined precipitously from the late 1960s to the late 1970s (Fig. 4; Table 1). Catches increased slightly from 1978 to 1981, but remained low. Present annual catches are only about 1/10 as large as the annual catches during

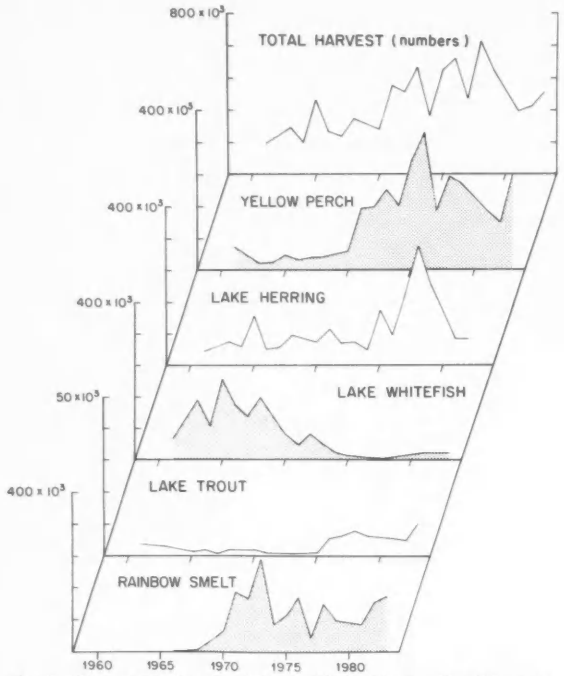

FIG. 2. Catch of fish (numbers) for the 70-d winter angling fishery on Lake Simcoe for 1961–83. Catches are uncorrected for variation in angler effort.

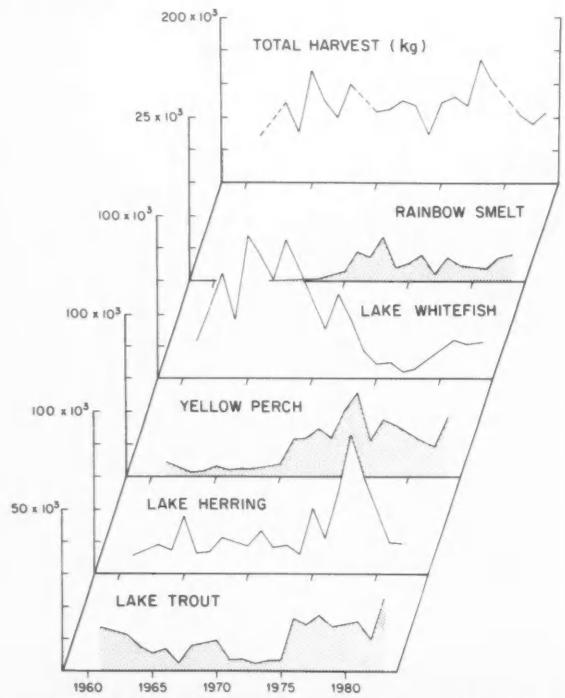

FIG. 3. Catch of fish (kg) for the 70-d winter angling fishery on Lake Simcoe for 1961–83. Catches are uncorrected for variation in angler effort.

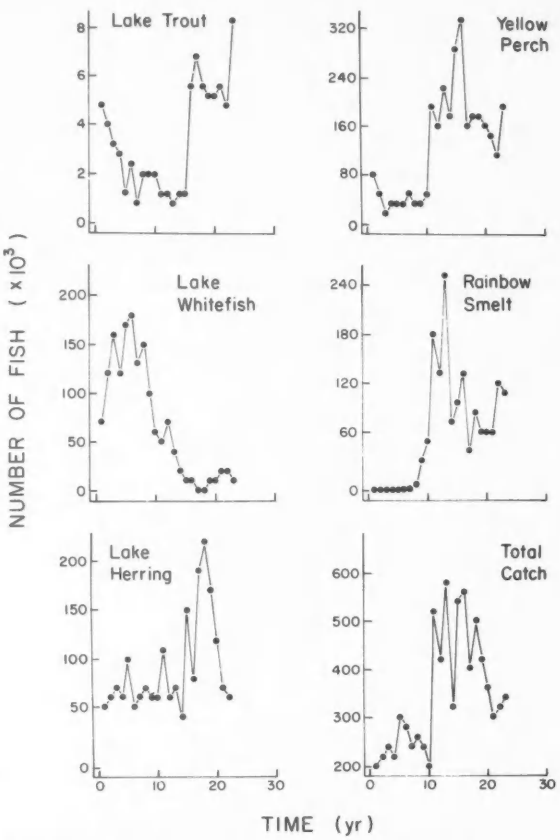

FIG. 4. Catch of fish for the 70-d angling season on Lake Simcoe, 1961–83, adjusted to the mean annual angling effort over all years.

the mid-1960s (Table 1). The biomass of lake whitefish caught indicates a greater relative increase in recent years (Fig. 8) compared with the numbers of fish caught (Fig. 5). This is due to increased growth rate and larger mean body size of the fish at the present low population density (Willox 1985; Evans et al. 1986). Evidence of complete recruitment failure during the early to mid-1970s is clear (Evans 1978). Some survival of young fish is known to have occurred during 1978 and 1979 (Willox 1985), but reproductive success remains very low to the present time.

Variability of lake whitefish catches about their trend is the lowest of the five species considered (Fig. 6); deviations vary by about ±25% of the trend, but this is a function of the lack of recruitment during most of the study period. The whitefish catch series is characterized by an early period of strong recruitment (1960–70) and a later period of exponential decline (1970–78), with a slight recovery during the late 1970s (Fig. 4 and 5).

Catches during the early 1960s ranged from about 50 000 to 160 000 whitefish·yr^{-1} (Fig. 4). Reproductive failure probably only began with the 1966 year-class, as expressed in the 1972 angler catch (Fig. 4). The downward trend in catch, from 1966 to 1970, appears to be circumstantial, an inevitable consequence, following the occurrence of a few very strong year-classes. Estimates of year-class strength, based on scale-age

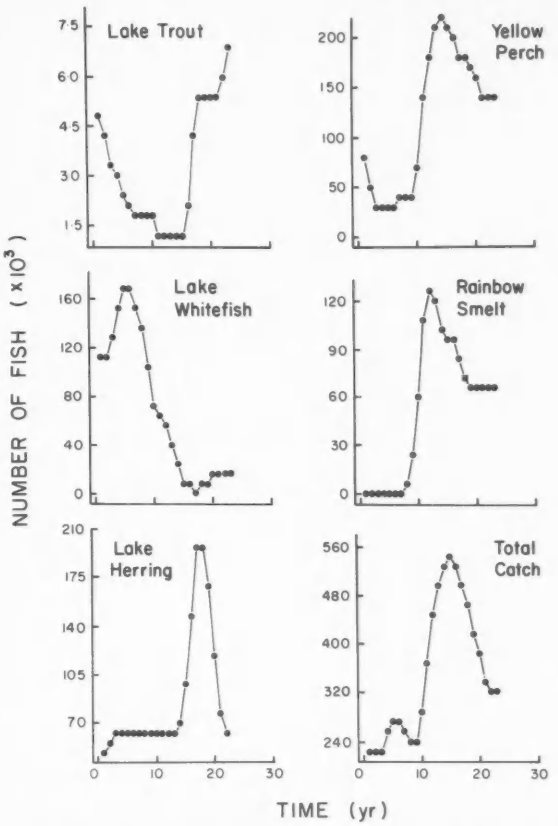

FIG. 5. Smoothed catch series in numbers of fish adjusted to a 70-d season and the mean annual level of angling effort for the winter angling fishery on Lake Simcoe, 1961–83. A compound smoother (3 RSSH, twice; Velleman and Hoaglin 1981) was applied to obtain the trend lines. Year 0 corresponds to 1960.

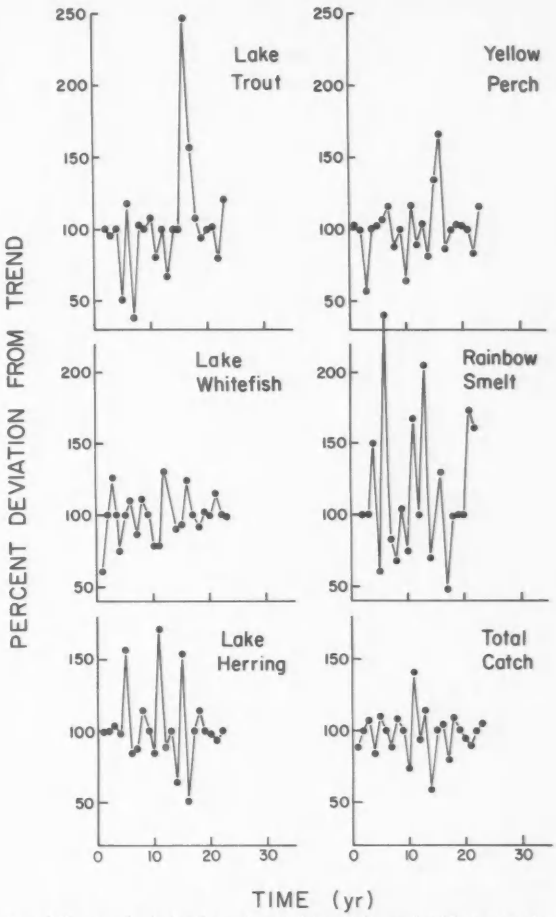

FIG. 6. Percent deviation from the catch trends for each of the species in the winter angling catch on Lake Simcoe, 1961–83, based on the smoothed curves in Fig. 5. Actual catches are shown as a percentage of the trend value.

data for angler-caught whitefish, also indicate that reproductive failure began about 1966.

Lake Herring

Lake herring catches increased threefold during the late 1970s from a relatively stable catch of 60×10^3 fish·yr^{-1} during the 1960s and early 1970s (Fig. 4 and 5; Table 1). Strong year-classes were produced during 1970–73 (Willox 1985) at the time of negligible reproductive success by lake whitefish. This is reflected in the catches of both species from 1977 and 1978, since mean age of both species in the winter catches is similar (6–8 yr). During the early 1980s, lake herring catches returned to levels typical of the 1960s (Fig. 4 and 5). Variability of the lake herring catches about the trend is relatively large compared with the other species, varying between ±50% of the trend (Fig. 6).

Yellow Perch

Catches of yellow perch increased sevenfold from about 3.5×10^4 fish·yr^{-1} during the 1960s to 2.4×10^5 fish·yr^{-1} during the late 1970s (Fig. 2; Table 1). Subsequently, catches declined to about 1.7×10^5 fish·yr^{-1} during the early 1980s. The trend in relative catch indicates that abundance of yellow perch has shifted from a low equilibrium to a new, higher equilibrium level from the beginning to the end of the study period (Fig. 4 and 5). Trends in the relative catches of yellow perch are parallel and roughly synchronous with those for rainbow smelt. Trends for yellow perch and lake whitefish appear to be approximately the inverse of one another. The irregular component of variation in yellow perch catches varies between ±35% of the trend (Fig. 6).

Rainbow Smelt

Rainbow smelt were first reported in Lake Simcoe in 1961 (MacCrimmon et al. 1983) and were first seen in the winter creel survey in 1964 (total estimated catch was 288 fish). The annual catch increased dramatically during the late 1960s and reached a peak of about 240 000 fish in 1973 (Fig. 2). The effort-corrected catch indicates that the relative abundance of smelt declined after 1973, the catch fluctuating between 3.5×10^4 and 1.2×10^5 fish·yr^{-1} from 1974 to 1983 (Fig. 4 and 5). Increase in the annual catch of smelt coincides closely with the decline in lake

TABLE 2. Summary of the effort-corrected catches (number of fish in thousands) and approximate variance components for the major species in the winter fishery, 1961–83. Percentages of total variance due to the trend and residuals are based on the smoothed curves and deviations shown in Fig. 5 and 6.

Species	Annual catch		Mean catch ± SD	Coefficient of variation (%)	Component of total variance (%)	
	Minimum	Maximum			Trend	Residual
Lake trout	0.7	8.2	3.3± 2.3	69.7	76.2	23.8
Lake whitefish	3.7	183.0	65.2±63.0	96.6	93.2	6.8
Lake herring	44.9	224.3	91.4±53.0	58.0	76.7	23.3
Yellow perch	18.7	334.7	132.5±91.2	68.8	77.9	22.1
Rainbow smelt	0	246.2	69.7±68.6	98.5	61.4	38.6
Total catch	200.0	574.8	357.4 125.5	35.1	74.0	26.0

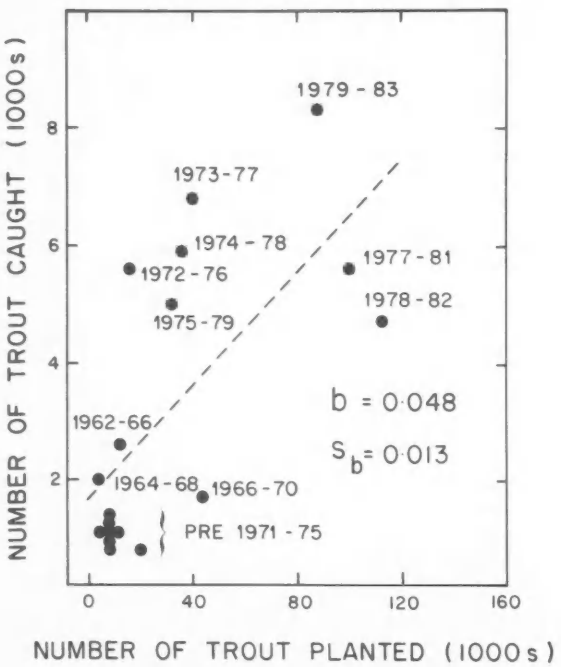

FIG. 7. Relationship between the number of yearling lake trout stocked and the number of lake trout harvested 4 yr later. Fry plantings were standardized to equivalent numbers of yearlings using a discount rate of 10 to 1 (Plosila 1977). Dates indicate the year of stocking and the year of peak capture which, on average, is 4 yr later. Performance of individual year-classes is not revealed here because several year-classes contribute to each year's harvest. Slope (b) and standard error of the slope (S_b) of the broken line are indicated.

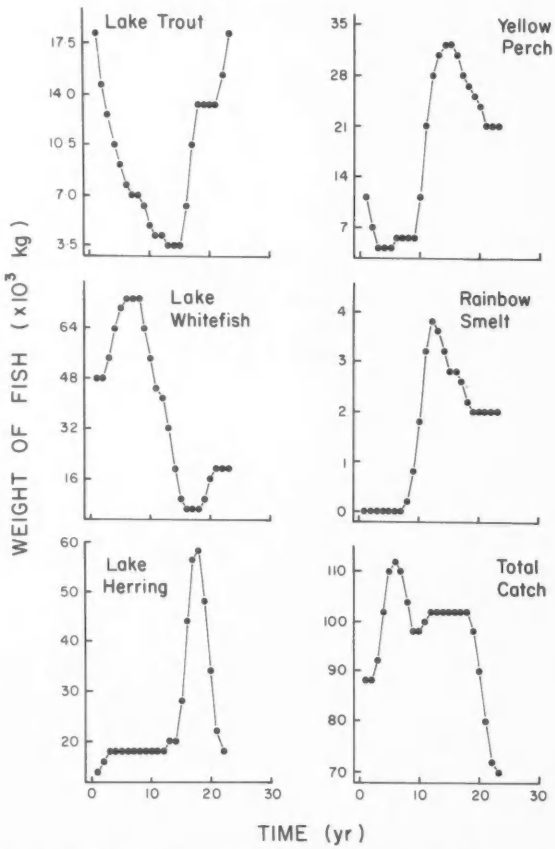

FIG. 8. Smoothed catch series of fish (kg) adjusted to 70-d season and the mean annual level of angling effort for the winter angling fishery on Lake Simcoe, 1961–83. Smoothing and axes as in Fig. 5.

whitefish, but appears to be completely uncoupled from changes in the catches of lake herring (Fig. 4 and 5). Variation in the annual catches of smelt is greater than for any of the other species, varying from 50 to 250% of the trend.

Total Catch

Total relative catch (number of fish) increased during the study period (Fig. 4) and appears to have reached a level which is about 30% higher than during the "pre-smelt period" in the 1960s. The total relative biomass of the annual catch, however, has actually declined (Table 1; Fig. 8). Larger numbers of small fish (yellow perch and rainbow smelt) have apparently replaced the formerly abundant, larger lake whitefish. Decline in the total annual biomass of the catch is probably due to a lower level of catchability for rainbow smelt, rather than a decline in total fish

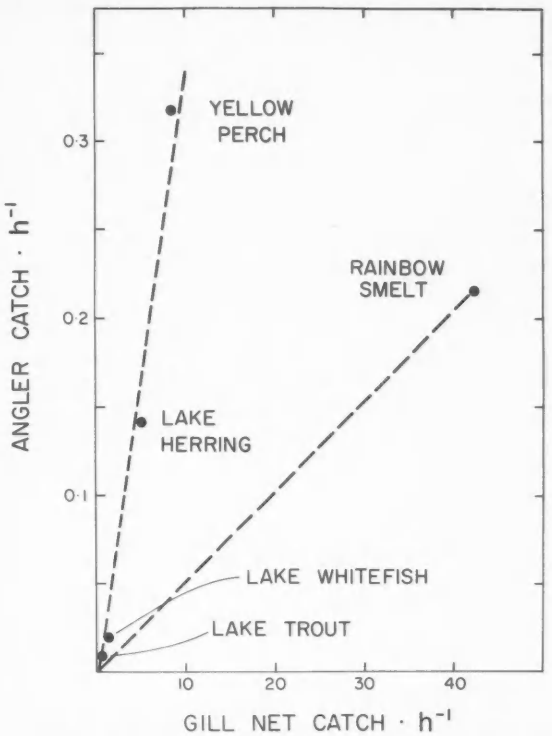

FIG. 9. Relationships between angler catch per hour during winter 1983 and mean daytime catches in multimesh, monofilament gillnets at 5, 10, 15, 20, 25, and 30 m during September 1982. Gillnet catches are means over all depths and replicates (four at each depth).

biomass in the lake. Rainbow smelt are usually caught incidentally while anglers are fishing for other species. Comparison of multimesh gillnet catches from the fall of 1982 with angler catches during the winter immediately following reveals (Fig. 9) that smelt are much more abundant than the angling data actually indicate. We assume that catchability in the nets is similar for each species, although this is not strictly true, small fish generally being less vulnerable than larger ones (Hamley 1975). Correction for selectivity would shift rainbow smelt even further to the right in Fig. 9 (Rudstam et al. 1984). Catchability of angling gear for the other species is similar and much higher than for smelt. Extrapolating the relationship for other species in Fig. 9 suggests that smelt are at least seven times more abundant than indicated by angler catches.

Variation of the total catch about the trend is relatively low, but the variability did increase substantially for about 5 yr during the early 1970s (Fig. 6). This increase corresponds with the period of exponential growth of the smelt population and is caused by the large changes in relative abundance that occurred in lake whitefish, yellow perch, and lake herring at about the same time. Invasion by smelt, therefore, appears to be associated with changing relative abundances of other species (trends) and with changes in the irregular component of the total catch. This conclusion provides support for hypothesis 1, but the disruptive effect of smelt on variation in total catch appears to be temporary. Shifts in the levels of abundance of the various species (trend component of variation), however, do appear to be persistent. This aspect is explored further in the following sections.

Intraspecific Interactions

Gradually declining positive ACRs with increasing lags were found for the catch series of each species. Significant PACRs, however, cut off abruptly after a lag of 1 yr (Table 3), indicating positive correlation between catches in adjacent years only. This suggests that year-classes, whether strong or weak, have a persistent effect on the catch for about 2 yr, on average, for each species. Another explanation is that the trends, which account for the majority of the total variance of each species (Table 2), cause adjacent residuals to be correlated.

Significant negative PACRs of the first differences of the effort-corrected catches were found for lake herring (1- and 5-yr lags), yellow perch (6-yr lag), and rainbow smelt (1-yr lag), suggesting intraspecific density-dependent recruitment (Table 3). Significant correlations (PACRs) at 1-yr lags for lake herring and rainbow smelt catches suggest interactions between adjacent year-classes, probably between yearlings and young-of-the-year, which explain about 11 and 29% of their variances, respectively. A significant PACR for lake herring at a 5-yr lag suggests a relationship between parent stock density and year-class success, which explains about 11% of the variation in catch. A significant PACR of -0.437 for yellow perch at a 6-yr lag indicates that about 19% of the total variation in their abundance is accounted for by a stock–recruitment relationship (i.e. transfer of variation from one generation to the next).

Significant negative PACRs were not found among the first differences of the effort-corrected catches for lake trout or lake whitefish, but a positive PACR (3-yr lag) was found for the latter species. This may be due to the dominating effect of the trend component in the whitefish catch series.

Interspecific Interactions

Correlation analyses of the catch series for the 10 possible pairwise species comparisons at time lags of ± 0–8 yr revealed only five statistically significant interspecific correlations after adjustment for autocorrelation within each catch series (Table 3). Adjustment for autocorrelation is necessary from a statistical perspective, but this procedure imposes a very restrictive constraint on the interpretation of the data. The trend component, which in part causes the autocorrelation, explains the majority of the variance in the catches of each species (Table 2). In theory, these trends could be caused by the effects of competitive or predatory interactions on species abundances. Elimination of the majority of the variation in the catches by statistically removing the autocorrelation in the data (by either adjusting the effective sample size or by differencing) increases the probability of overlooking real effects (i.e. of accepting a false null hypothesis or committing a type II error). In view of the difficulties of interpreting correlations between autocorrelated time series, our statistical approach is primarily exploratory and designed to identify potentially causal relationships between species. Ranks and natural logarithmic transformations have been used to approximate normal bivariate distributions of species composition in the catches.

Negative correlations exist between lake whitefish and each of the other four species (Table 3), but only the correlation with rainbow smelt is statistically significant (Fig. 10). Strong negative correlation occurs between lake whitefish and yellow perch catches but, due to high autocorrelation in both series, is

TABLE 3. Spearman rank correlation coefficients (r_s) for pairwise interspecific comparisons of the winter angling catches of lake trout (LT), lake whitefish (LW), lake herring (LH), yellow perch (YP), and rainbow smelt (RS). Partial autocorrelation coefficients for first differences of the catches are indicated for intraspecific comparisons. The leading species is the one that has been shifted forward in time. Only significant correlations are indicated (*$P < 0.05$; **$P < 0.01$). Tests of significance have been corrected for autocorrelation effects. Sample size decreases as lag time increases.

Species	Lag (yr)	Leading species (r_s) LT	LW	LH	YP	RS
LT	0	—	−0.511	0.337	0.062	−0.110
	1	−0.074	−0.670	0.554	0.234	0.085
	2	0.043	−0.686	0.128	0.428	0.089
	3	−0.109	−0.650	0.237	0.648	0.347
	4	−0.016	−0.716	0.308	0.741	0.568
	5	−0.172	−0.708	0.372	0.809	0.746
	6	−0.035	−0.735	0.509	0.674	0.757
	7	0.325	−0.799	0.088	0.775	0.785
	8	0.194	−0.791	0.207	0.755	0.774
LW	0	−0.511	—	−0.542	−0.759	−0.582
	1	−0.422	−0.070	−0.339	−0.762	−0.615
	2	0.022	−0.109	−0.371	−0.863	−0.749
	3	0.219	0.415*	−0.100	−0.880	−0.833
	4	0.402	−0.135	−0.282	−0.849	−0.901*
	5	0.318	−0.090	−0.212	−0.659	−0.859*
	6	0.358	−0.158	−0.364	−0.546	−0.803
	7	0.412	−0.035	−0.227	−0.448	−0.752
	8	0.446	−0.261	−0.006	−0.364	−0.418
LH	0	0.337	−0.542	—	0.363	0.254
	1	0.457	−0.625	−0.324*	0.194	0.011
	2	0.241	−0.571	0.064	0.576	0.308
	3	−0.068	−0.323	−0.101	0.431	0.382
	4	−0.527	−0.258	−0.087	0.641	0.462
	5	−0.445	−0.047	−0.326*	0.341	0.607
	6	−0.694	−0.146	−0.132	0.380	0.562
	7	0.085	−0.184	0.155	0.196	0.487
	8	0.064	0.401	0.463	−0.164	−0.422
YP	0	0.062	−0.759	0.363	—	0.834*
	1	−0.086	−0.639	0.062	−0.224	0.719
	2	−0.284	−0.602	0.164	−0.147	0.816*
	3	−0.354	−0.318	0.076	−0.025	0.797*
	4	−0.530	−0.262	0.205	0.061	0.665
	5	−0.286	−0.124	0.037	0.246	0.472
	6	−0.293	−0.056	0.057	−0.437*	−0.019
	7	−0.074	0.108	0.166	−0.217	0.283
	8	0.064	0.401	0.463	−0.164	−0.422
RS	0	−0.110	−0.582	0.254	0.834*	—
	1	−0.179	−0.452	0.004	0.548	−0.537**
	2	−0.320	−0.435	0.015	0.567	0.025
	3	−0.222	−0.249	0.230	0.328	0.177
	4	−0.267	−0.197	0.210	0.210	−0.275
	5	−0.087	−0.039	0.262	0.006	−0.165
	6	−0.055	−0.136	−0.044	−0.258	−0.095
	7	0.053	0.110	0.373	−0.046	−0.034
	8	0.547	0.394	0.129	−0.616	−0.280

not statistically significant (Fig. 11). Both rainbow smelt and yellow perch are negatively correlated with lake whitefish at biologically meaningful time lags, however, supporting the hypotheses that causal relationships exist between their populations. Whitefish are negatively correlated with smelt catches 4–5 yr earlier which, based on mean ages in the catch of 6–8 and

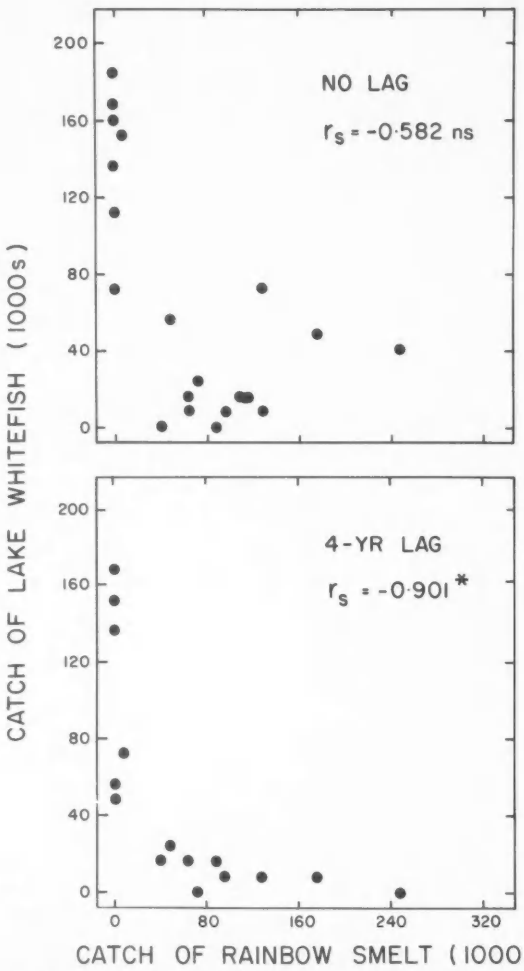

FIG. 10. Catches of lake whitefish versus the catches of rainbow smelt in the Lake Simcoe winter fishery, 1961–83. The upper plot compares catches in the same calendar year. The lower plot compares catches of rainbow smelt with catches of lake whitefish 4 yr later. Spearman rank correlation coefficients (r_s) are from Table 3. Tests of r_s are adjusted for autocorrelation.

2–3 yr, respectively, suggests a negative interaction between year-classes originating in the same year (Table 4). This correlation could only be expressed in the fishery by a competitive interaction at age 0, smelt being dominant (Table 5). Whitefish catches are most strongly correlated with yellow perch catches 0–3 yr earlier (Table 4), indicating possible competition or predation at age 0 or between age 0 and yearlings (Table 5). A significant positive correlation exists between yellow perch and rainbow smelt (0- to 3-yr lag, smelt leading; Table 3; Fig. 12). Negative interaction between these species and lake whitefish possibly results in mutual enhancement of their survival rates.

Discussion

Effects of physical factors on the metabolism, activity, and

TABLE 4. Correlation coefficients between the catches of rainbow smelt (RS), lake whitefish (LW), and yellow perch (YP) using the effort-corrected data transformed to natural logarithms and ranks. The strongest correlations in each case are underlined, and asterisks indicate statistical significance ($P < 0.05$) after correction for autocorrelation in the raw data. Sample size is indicated in parentheses.

Species comparison	Data treatment		Time lag (yr)								
Leading × lagging	Transform	Coefficient	−2 (16)	−1 (16)	0 (20)	1 (16)	2 (16)	3 (15)	4 (15)	5 (14)	6 (13)
RS × LW	$\log_e$	r_s	−0.288	−0.436	−0.599	−0.673	−0.716	−0.725	−0.739	−0.704	−0.601
	Ranked	r_s	−0.435	−0.452	−0.582	−0.615	−0.749	−0.833	−0.901*	−0.859*	−0.803
YP × LW	Log_e	r	−0.608	−0.751	−0.823	−0.817	−0.851	−0.807	−0.701	−0.545	−0.373
	Ranked	r_s	−0.602	−0.639	−0.759	−0.762	−0.863	−0.880	−0.849	−0.659	−0.546
RS × YP	Log_e	r	0.320	0.453	0.692	0.805*	0.847*	0.748	0.652	0.587	0.466
	Ranked	r_s	0.567	0.548	0.834*	0.719	0.816*	0.797*	0.665	0.472	−0.019

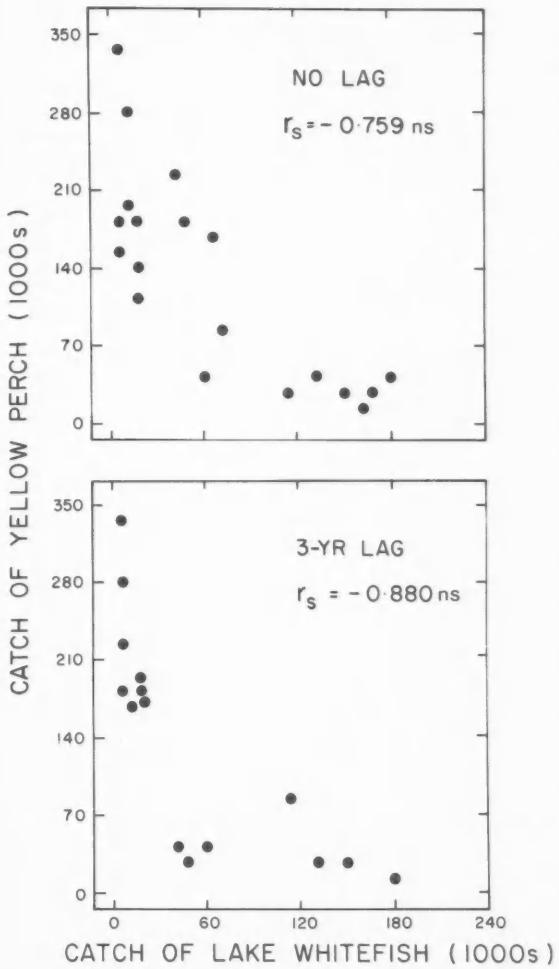

FIG. 11. Catches of yellow perch versus the catches of lake whitefish in the Lake Simcoe winter fishery, 1961–83. The upper plot compares catches in the same calendar year. The lower plot compares catches of yellow perch with catches of lake whitefish 3 yr later. Spearman rank correlation coefficients (r_s) are from Table 3. Tests of r_s are adjusted for autocorrelation.

survival of fishes are well known, as are their effects on geographic distributions and local abundances of species. While studies showing the effects of physical factors on recruitment success are relatively few (e.g. Christie and Regier 1973; Le Cren et al. 1977), it seems certain that such factors play a significant role in determining community structure and productivity. The effects of intraspecific, density-dependent recruitment are also established for some species (e.g. Healey 1980; Jensen 1981; Henderson et al. 1983). More recently, interspecific interactions have also been recognized to influence fish species abundance (e.g. Svardson 1976; Ursin 1982; Jones 1982; Skud 1982). Three primary sets of factors, therefore, influence species abundances and, hence, the structure of fish communities: physical–environmental factors, intraspecific factors, and species interactions. Our analyses focus on the latter two factors but implicitly recognize that these operate within a broader set of constraints imposed by the physical environment.

Causes of Variation in Species Abundance in Lake Simcoe

Lake trout

Abundance of lake trout in Lake Simcoe declined during the 1950s, due to recruitment failure, as indicated by increasing mean body size and increasing occurrence of hatchery fish in the catch (DesJardine and Lawrence 1979). The precise contribution of the hatchery fish during the 1960s is impossible to assess, however, because the vast majority of fish planted from 1950 to 1965 were either unmarked fry or fingerlings. Stocking rates varied from 11 000 to 240 000 during the 1950s, although the rates were relatively constant from 1953 to 1963 (MacCrimmon and Skobe 1970, p. 55), which would correspond to the period of declining recruitment to the fishery during the 1960s and early 1970s. This indicates that the decline was due to failing natural reproduction. Yearling trout were stocked annually beginning in 1965 (with the exception of 1967). After 1973, the number of yearlings stocked each year increased by 4 to 5 times, higher catches during the late 1970s and 1980s being the result (Fig. 7). Planting of hatchery trout accounts for about 52% of the variation in relative catch. Different parental stocks were introduced during the 1970s, which probably also accounts for a significant additional component of variation in the catch (MacLean et al. 1981; Willox 1985).

Cause of the lake trout decline is unknown, but would not appear to be due to the effects of other fish species or to exploitation by angling. An increasing proportion of large fish

TABLE 5. Comparison of possible negative interactions between rainbow smelt (RS) and lake whitefish (LW), and between yellow perch (YP) and lake whitefish (LW) showing the expected time lags that would occur for these effects to be expressed in the winter catches when the mean ages are 6–8 yrs for lake whitefish, 5–7 yrs for yellow perch, and 2–3 yrs for rainbow smelt. The leading species (with reference to catch) is indicated in parentheses for each interaction. Life stage abbreviations: YOY, young-of-the-year; YRLG, yearling.

Species comparison			Expected lag time (yr)				
Dominant	vs.	subordinate	YOY vs. YOY (competition)	YRLG × YOY (competition predation)	Preadult vs. YOY (predation)	Adult vs. YOY (predation)	Adult vs. egg (predation)
RS	vs.	LW	4–5 (RS)	5–7 (RS)	5–7 (RS)	6–8 (RS)	7–9 (RS)
LW	vs.	RS	4–5 (RS)	3–4 (RS)	0	2–3 (LW)	3–4 (LW)
YP	vs.	LW	0–2 (YP)	2–3 (YP)	3–5 (YP)	6–8 (YP)	7–9 (LW)
LW	vs.	YP	0–2 (YP)	0	1–4 (LW)	5–7 (LW)	6–8 (LW)

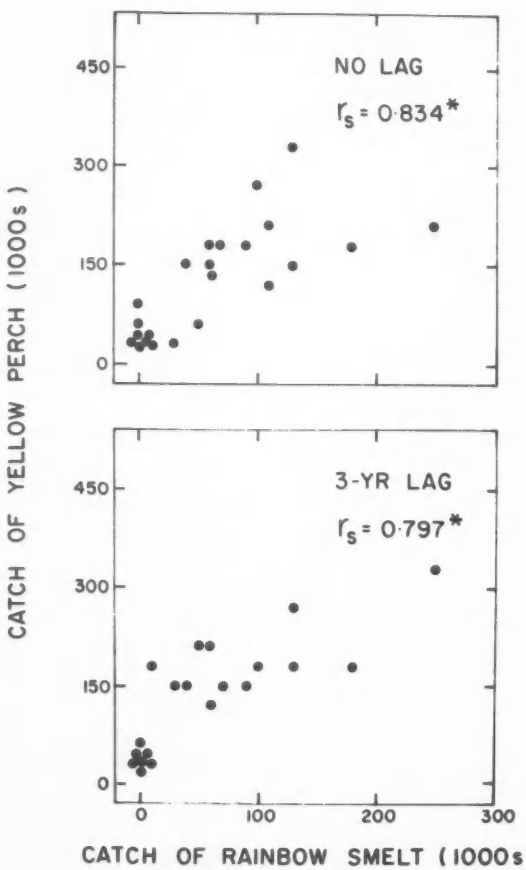

FIG. 12. Catches of yellow perch versus the catches of rainbow smelt in the Lake Simcoe winter fishery, 1961–83. The upper plot compares catches in the same calendar year. The lower plot compares catches of rainbow smelt with catches of yellow perch 3 yr later. Spearman rank correlation coefficients (r_s) are from Table 3. Tests of r_s are adjusted for autocorrelation.

in the catch during the 1960s and 1970s indicates an ageing population and suggests that reproductive failure is the cause of the decline. Deteriorating water quality, degradation of nearshore spawning habitat, and low egg survival would appear to be the most probable causes of reproductive failure. Viable gametes are known to be produced (based on hatchery results), indicating that in situ survival of either the eggs or young-of-the-year (or both) is very low.

Lake trout have been heavily exploited, at least since the mid-1880s, and supported early commercial yields of 0.241–0.256 $kg \cdot ha^{-1} \cdot yr^{-1}$ for a 30-yr period from 1870 to 1899 (MacCrimmon and Skobe 1970). After 1900, gear restrictions reduced exploitation dramatically and the population remained relatively strong, at least until the mid-1920s (Rawson 1930). Present harvests of 0.16 $kg \cdot ha^{-1} \cdot yr^{-1}$ are based almost entirely on captures of hatchery fish and would appear to be well below the productive capacity of the lake and less than most other lake trout lakes in Ontario (Martin and Olver 1980). Of course, water quality and habitat availability now impose limitations that probably did not exist 80–100 yr ago. The apparent reduction in contribution to the fishery at very high stocking rates is possibly due to density-dependent survival associated with the practice of releasing the fish at a single site each year. This would result in very high density in localized areas and perhaps reduced survival in years when large numbers of fish are released.

Invasion of Lake Simcoe by rainbow smelt does not appear to have been responsible for the reproductive failure of lake trout; declining abundance of trout during the 1960s precedes the smelt invasion. Yearling lake trout of hatchery origin have been very successful in the presence of high densities of rainbow smelt, but very few trout have been produced by natural reproduction since the early 1970s (DesJardine and Lawrence 1977, 1979). We are unable to entirely eliminate smelt as a possible factor in the continued reproductive failure of the lake trout, but the existing evidence does not support this hypothesis.

Lake Simcoe lake trout prey primarily on rainbow smelt and lake herring and, to a lesser extent, on emerald shiner, *Notropis atherinoides*, and yellow perch (DesJardine and Lawrence 1979; Burns 1985). Declines in abundances of lake herring and rainbow smelt, which occurred in the mid- to late 1970s, may, in part, have been due to increased predation by trout (Fig. 4). Similarly, depression of prey species populations by salmonid

predators has been observed in Lake Michigan (Stewart et al. 1981) and Lake Ontario (Christie et al. 1987). Decline in yellow perch abundance, however, would not appear to be due to lake trout predation, given the low status of perch in the trout diet, even though shifts in their abundances are negatively correlated during the late 1970s (Fig. 4).

Lake whitefish

Total variation in the catches of lake whitefish is largely due to an exponential decline in abundance during the study period (trend component, Table 2). Recruitment failure is well documented in this population (Evans 1978; Evans et al. 1986), but the cause is unknown. Fecundity of the females and viability of the eggs appear to be normal (Evans 1978), and larval whitefish continue to be produced each spring, although early (1960s) data are not available for comparison of relative abundances of larvae over years (DesJardine 1979). Tagging studies revealed that fishing mortality for lake whitefish was only about 10–15%·yr^{-1}, indicating that overexploitation is not the cause of recruitment failure. Healthy populations can support exploitation at several times this level (Healey 1975). The general effects of eutrophication, including reduced hypolimnetic oxygen levels, deterioration of spawning shoals, and increased numbers of fish and invertebrate predators, are other factors, but they do not appear to account for the whitefish decline, nor do chemical contaminants (Evans et al. 1986). Recent plantings of hatchery-reared, yearling lake whitefish (1982–85) have survived and grown well in Lake Simcoe, indicating that reproductive failure occurs due to mortality prior to the yearling stage.

Recruitment failure of lake whitefish is closely correlated with the introduction of rainbow smelt in about 1960 and rapid increase in their abundance during the late 1960s. A 4-yr lag (rainbow smelt leading) indicates a possible competitive interaction between age 0 lake whitefish and rainbow smelt. Young lake whitefish are pelagic during the larval stage, but move to the lake bottom by July of their first year (Hart 1930; Reckahn 1970). During the late summer, young whitefish were captured above the thermocline in the vicinity of the 17°C isotherm in South Bay, Lake Huron, and were found to prey primarily on zooplankton, dipteran larvae, and ostracods (Reckahn 1970). Young rainbow smelt have a similar distribution and diet during late summer (MacCrimmon and Pugsley 1979; Evans and Loftus 1987). Rainbow smelt are very fecund, an average of 20 000 to 30 000 eggs being produced by each female each year (Bailey 1964; Pugsley 1976) compared with 15 000 to 25 000 for whitefish (Semple 1968; Evans 1978). By the early 1970s, when the smelt population was nearing its peak abundance in Lake Simcoe, enormous numbers of young smelt must have been present. In Lake Simcoe, age 0 smelt attain a length of about 110 mm by age 1 (Pugsley 1976) compared with about 126 mm for lake whitefish (Semple 1968). Age 0 smelt, being almost as large as age 0 whitefish and probably many times more abundant in the early 1970s, would have placed a huge additional load on the food and space resources of the deep epilimnetic zone. Competition at that time may have resulted in displacement of lake whitefish from their preferred habitat, resulting in elevated mortality. How such displacement could result in mortality is not known, but low oxygen concentration in the hypolimnion during late summer (Evans 1978), and congregation of predators in the region of the thermocline as a result, would severely limit the availability of favorable habitat for young whitefish.

If a competitive interaction between the young of these species resulted in reproductive failure of lake whitefish, a close correlation, but with a 4-yr lag, should exist between the period of exponential growth of the smelt population (1968–73) and the period of exponential decline of the whitefish population (1972–77) (Fig. 4). The negative relationship during this period is very strong, the 4-yr lag corresponding to the difference in mean ages of the two populations. Mean age is a relatively crude measure of year-class representation in the catches, however. Predation by yearling or adult smelt on larvae or age 0 whitefish (5- or 6-yr lag, Table 5) might also, in part, explain the changes in abundance of lake whitefish. Adult smelt are reported to prey on the larvae of lake whitefish and lake herring under some circumstances (Loftus and Hulsman 1986), and probably do so to some extent in Lake Simcoe. Smelt predation, however, has not had a significant effect on recruitment success of lake herring. This suggests that predation on the larvae of these species is not a major cause of early mortality in Lake Simcoe. Young lake herring continue a pelagic existence throughout their first year (Fry 1937), while whitefish become demersal at about 6–8 wk after hatching. The presumptive effect of smelt on lake whitefish survival, therefore, must occur after their descent to the lake bottom.

Lake herring

Intraspecific density-dependent effects account for a significant component of the variation in abundance of lake herring. PACR at a 1-yr lag indicated negative interaction between yearling and age 0 smelt and explains about 11% of the total variation. Yearling lake herring remain suspended in the water column, suggesting the possibility of competition for prey with the young-of-the-year, both groups being planktivorous and occurring in the vicinity of the thermocline (Fry 1937). Negative correlation between catches at a 5-yr lag time also explains about 11% of the total variance. This correlation indicates a stock–recruitment relationship, stock size being negatively correlated with the size of the stock 5 yr later. Definitive information on age of maturity is not available, but eight 3-yr-olds (5 males, 3 females) and five 4-yr-olds (4 females, 1 male), observed during September 1982 and 1983, were maturing. Similarly, the majority of lake herring in nearby Lake Huron had reached maturity at 3–4 yr (Van Oosten 1928). Five years would appear to be about the generation time of lake herring in Lake Simcoe, being about the mean age of all spawners.

Predation on age 0 lake herring by adults is one possible mechanism which might explain the apparent stock–recruitment relationship. Adult lake herring have been observed to prey on coregonine larvae (Hart 1930; Pritchard 1931), although larval coregonines have not been found in lake herring guts in Lake Simcoe (Day and DesJardine 1975).

Abundance of lake herring increased from 1976 to 1979, corresponding to strong year-classes produced in 1970, 1971, 1972, and 1973 (Willox 1985). Low catches during 1981 and 1982 are typical of catches during the 1960s and do not appear to signal a major change in the long-term recruitment pattern. As noted, however, lake trout predation could have caused an increase in lake herring mortality during the late 1970s and a corresponding decline in catch.

Production of strong year-classes of lake herring, from 1970 to 1973, corresponds with the period of very weak whitefish year-classes and low abundance of lake trout. Lake herring and whitefish catches are negatively correlated ($P > 0.05$), correla-

tion being strongest at a 0- to 1-yr lag (lake herring leading, Table 3). Median ages are similar for these species, indicating possible interactions either between the young-of-the-year or between yearling lake herring and age 0 whitefish. These species share the same pelagic habitat and food supply during the larval stage; therefore, it is possible that the abundance of one species could affect the early success of the other through competition at that time. Larval whitefish were presumably relatively abundant during the early 1970s, however, even though their survival and contribution to the adult stock was negligible (DesJardine 1979). Absence of competition between lake herring and lake whitefish larvae, therefore, appears to be an untenable explanation for strong herring year-classes from 1970 to 1973.

Reduced interaction between yearling lake whitefish and age 0 lake herring or vice versa could also possibly explain the occurrence of strong year-classes of lake herring during 1970–73, although no evidence exists to suggest the occurrence of these interactions. Age 0 lake whitefish and yearling lake herring are primarily planktivores, but occupy benthic and midwater habitats, respectively (Hart 1930; Fry 1937; Reckahn 1970). Similarly, postlarval lake herring and yearling lake whitefish are also spatially segregated.

Lake trout abundance was low during the 1970–73 period of strong lake herring recruitment, but had been low for several years, suggesting that low lake trout density alone was not the factor that led to increased herring production. We speculate that a combination of reduced predation by lake trout and low abundance of lake whitefish may have contributed to increased survival of lake herring during 1970–73.

Production of lake herring in Lake Simcoe does not appear to be directly affected by the abundances of yellow perch or rainbow smelt. The latter observation is significant in view of frequent speculations (e.g. Anderson and Smith 1971; Christie 1974; Selgeby et al. 1978) and observations (Loftus and Hulsman 1986; Evans and Loftus 1987) to the contrary, in other lakes. In Swedish lakes, cisco, *Coregonus albula*, and smelt, *Osmerus operlanus*, occur sympatrically in only 13 of 110 lakes in which either one or the other species is present (Svardson 1976). In addition, cisco occurred in 71 lakes and smelt in 51 which, when interpreted on the basis of geographic and distributional information, led Svardson (1976) to conclude that the cisco is dominant over smelt. This was also found to be the situation in the brackish waters of Bothnia Bay (Enderlein 1981).

Production of strong year-classes of lake herring, coincident with high densities of rainbow smelt during the early 1970s, indicates that predation by smelt on lake herring larvae has not been of major significance in Lake Simcoe. Similarly, this applies to predation of lake herring larvae by yellow perch, which were also abundant during the early 1970s.

Yellow perch

Variation in yellow perch abundance appears to be strongly influenced by intra- and interspecific factors in Lake Simcoe. Intraspecific density-dependent effects account for about 19% of the total variation in catch. Year-class production in perch populations is typically very variable (Le Cren et al. 1977; Nielson 1980), and several hypotheses have been proposed to explain the recruitment process in this species, including effects of water temperature, water levels, intraspecific factors, and interspecific factors (Kipling 1976; Nielson 1980; Craig and Kipling 1983; Persson 1983; Henderson 1985). None of these studies has clearly described a stock–recruitment relationship, although Le Cren et al. (1977) concluded that density-dependent recruitment occurred in some years in Lake Windermere and Persson (1983) argued that intraspecific competition for food and space could limit the number and size of perch year-classes. Kipling (1976) and Goldspink and Goodwin (1979) also reported that cannibalism by adult European perch, *Perca fluviatilis*, on their young-of-the-year reduced survival in some years. Tarby (1974) also observed cannibalism by adult yellow perch in Oneida Lake, New York. Keast (1977) found that the diet of perch in Lake Opinicon, Ontario, shifted with age from zooplankton to benthic invertebrates to one exceeding 25% fish (volume) by age 5. Cannibalism, therefore, would appear to be a possible cause of the density-dependent recruitment of yellow perch in Lake Simcoe, although diet studies found very few young perch in the guts of adult Lake Simcoe perch (Day and DesJardine 1975; Burns 1985; Wilson and Burns 1985).

Correlation between yellow perch and whitefish catches (Table 4) suggests a competitive or predatory interaction between their young-of-the-year or between yearling lake whitefish and age 0 yellow perch (Table 5). In the Bodensee, where catches of the blaufelchen, *Coregonus wartmanni*, and the European perch were strongly negatively correlated, Numann (1972) suggested predatory interaction as the explanation, but was unable to decide which species preyed on the other. Neither predation hypothesis is consistent with our results (Table 5), and whitefish and yellow perch diets in Lake Simcoe provide no evidence of predation on each other at any life stage (Rawson 1930; Day and DesJardine 1975; Burns 1985). In Lake Vanern, Sweden, catches of whitefish (*Coregonus* spp.) and European perch also show an inverse abundance relationship, and in many Scandinavian lakes, perch and whitefish commonly prey on each other's young (Svardson 1976). Svardson concluded that whitefish are dominant in large, cool lakes and that yellow perch are dominant in small, warm lakes.

Our analysis indicates that the strongest correlation between yellow perch and lake whitefish is at lags of 0–4 yr (yellow perch leading, Table 4). Prior to 1970, lake whitefish were dominant over yellow perch. Since 1970, yellow perch have either become dominant over whitefish or have simply increased due to reduced interaction with whitefish. The latter interpretation is the most parsimonious, and we speculate that either competition or predation, or both, by age 0 or yearling lake whitefish on age 0 yellow perch may be the mechanism by which lake whitefish formerly dominated over perch.

Lake whitefish hatch during late April and early May in Lake Simcoe (DesJardine 1979), about 6 wk earlier than yellow perch. The exact timing of the transition of larval whitefish from a pelagic to benthic mode is uncertain but, based on studies elsewhere (Hart 1930; Rackahn 1970), probably occurs during mid- to late June. The pelagic distribution of age 0 whitefish, therefore, would overlap with larval yellow perch, which hatch during early to mid-June. Perch larvae are pelagic for 4–6 wk prior to moving inshore and becoming demersal (Lin 1983; Whiteside et al. 1985). During their pelagic phase, larval perch would be vulnerable to predation by age 0 and yearling whitefish, although no evidence is available to support this, except as noted earlier (Svardson 1976). A more probable interaction is competition for food and/or spatial displacement by larger age 0 and yearling whitefish, both groups having access to available zooplankton and benthic food resources of the epilimnetic zone prior to the appearance of each cohort of

age 0 yellow perch. Diets of both whitefish groups (Hart 1930; Reckahn 1970; Hoagman 1973) are similar to the diet of the age 0 yellow perch (Lin 1983; Whiteside et al. 1985). Age 0 whitefish also occupy benthic areas of the epilimnetic zone during summer (Hart 1930; Reckahn 1970). Overlap in distribution and diet between young whitefish and perch could result in competition, possibly explaining the negative correlation between these species. The importance of benthic food resources for recruitment of yellow perch is evident in the 15-fold increase in abundance of juvenile yellow perch which occurred following removal of 85% of the biomass of white sucker from Wilson Lake, Minnesota (Johnson 1977). The actual mechanism by which competition could result in mortality is unknown, but by affecting growth rate and body size of young perch, competition for food or displacement to unfavorable habitat could possibly reduce overwinter survival (Toneys and Coble 1979).

The alternative explanation that some external factor has caused a shift in competitive advantage between yellow perch and lake whitefish is equally well supported by our analysis (Table 5). Changes in climate and nutrient status were identified by Svardson and Molin (1981) as factors that could cause dominance shifts between fish species. Invasion by a third species might also cause a competitive advantage to be reversed through interference by the invader with the original dominant species. Invasion by rainbow smelt and increasing nutrient enrichment in Lake Simcoe (Ralston et al. 1975; Evans et al. 1986) would both tend to favor increased production of yellow perch rather than lake whitefish. Yellow perch are now numerically dominant over lake whitefish, but the actual mechanism, whether a passive increase in yellow perch, due to reduced competition from lake whitefish, or a reversal in competitive advantage, cannot presently be determined.

Rainbow smelt

Catches of rainbow smelt are the most variable of the species studied (Fig. 6). Intraspecific effects account for about 29% of the total variation in catch and indicate interaction between age 0 and yearling smelt. Similar alternating strong and weak year-class strength (Fig. 6) has been observed for Lake Erie smelt (Regier et al. 1969). These authors suggested that cannibalism by yearling smelt on age 0 smelt might be responsible for strong year-classes in alternate years. Cannibalism by rainbow smelt has been widely observed (Evans and Loftus 1987). In Lake Simcoe, age 0 smelt were preyed upon during most of the year by larger smelt, usually adults older than 2 yr (Pugsley 1976). Because of constraints on prey sizes that can be eaten, cannibalism by yearlings could only involve predation on the larvae during spring, a phenomenon which has not been observed.

A second possible explanation for alternating year-class strength is competition for food and space between yearlings and age 0 smelt. During the day, yearling rainbow smelt are generally found deeper in the epilimnion than age 0 smelt, while the adults occupy the hypolimnion (Ferguson 1965; MacCallum and Regier 1970). Diel vertical movements by yearling and age 0 smelt (Ferguson 1965; Brandt et al. 1980) results in greater overlap in their distributions at night. Diets of these age groups are similar, consisting primarily of zooplankton (MacCrimmon and Pugsley 1979), especially during the night when both groups are off the lake bottom. Direct competition between yearlings and younger smelt, therefore, seems probable.

Correlation between the relative abundances of smelt and lake whitefish appears to represent a causal relationship resulting in elevated mortality of young whitefish. In Lake Simcoe, complete reproductive failure of whitefish occurred during the early 1970s when smelt were very abundant (Evans 1978). In 1981, a few small whitefish (age 3 yr) were observed in the winter angling catch, indicating some survival by the 1978 year-class, the first verification of significant escapement since about 1970. Coincidentally, the abundance of adult smelt declined to its lowest level in 1977 subsequent to reaching peak density in 1973 (Fig. 4).

A review of 24 case studies of smelt invasions into lakes having indigenous lake whitefish populations revealed that recruitment failure of the latter species subsequently occurred in at least 13 cases (Evans and Loftus 1987). Recruitment failure of lake whitefish was the most common response following introduction of smelt. This provides further evidence, albeit circumstantial, that interaction between these species causes an increase in the natural mortality rate of lake whitefish.

Positive correlation between the catches of rainbow smelt and yellow perch would appear to be due to the common linkage of the recruitment processes of these species to interaction with lake whitefish. If lake whitefish compete simultaneously with yellow perch and smelt, as we suggest, a mutualistic relationship (both species benefit) would exist should they jointly reduce the abundance of lake whitefish. Increased predation on smelt by lake trout would reduce the negative effect of smelt on lake whitefish and, in turn, lessen the positive effect of smelt on yellow perch. Lake herring, as an alternate prey for lake trout, would buffer lake trout predation on rainbow smelt.

Conclusions

We are unable to reject our three main hypotheses and conclude that introduction of rainbow smelt has had a major influence on the structure of the Lake Simcoe fish community and on yields of individual species. A complex nexus of direct and indirect interactions appears to link all of the major species in the winter fishery. This is suggested by the sequence of changes in species abundances which occurred during the study period:

(1) Lake trout declined initially due to reproductive failure, possibly caused by poor survival of eggs and young as a result of eutrophication.

(2) Rainbow smelt successfully invaded the lake during the period of declining trout abundance, possibly due to reduced predation by trout.

(3) Lake whitefish declined due to complete reproductive failure during the period of exponential growth of the smelt population. Competition between their young or predation by adult smelt on young whitefish, or both, is the suspected cause, although predation appears to be of lesser importance.

(4) Yellow perch increased in abundance as lake whitefish density declined. It is not clear if attainment of dominance by yellow perch is due to a competitive advantage of yellow perch over lake whitefish in the presence of smelt, or is simply due to an increase in their abundance in the absence of competition from young whitefish. In either case, invasion by smelt has not had an adverse effect on yellow perch.

(5) Lake herring abundance increased when lake whitefish were at their lowest density, but subsequently they declined, possibly in response to increased predation by lake trout. Rainbow smelt also declined as lake trout density increased.

Total yield (biomass) to the winter fishery declined during the survey period, although it seems probable that total biomass of

fish in the lake remained relatively stable. Total yield to the fishery has declined because rainbow smelt have replaced whitefish, a species which contributed more to the anglers' catch. Annual variation in total yield also increased coincident with the initial increase in smelt abundance, but this effect was temporary, possibly due to the stabilizing influence of the subsequently increased abundance of lake trout.

Intraspecific, density-dependent effects on abundance were found for lake herring, yellow perch, and rainbow smelt. This capacity to regulate population density provides a mechanism by which these species can avoid very high densities at which they might otherwise entirely eliminate their prey.

Among the five species considered, a complex web of interactions, including predation and competition for food and space, presumably occurs between the various life stages. Lake trout, in particular, appear to have a pervasive influence on species composition. Manipulation of the density of lake trout, therefore, offers considerable potential for managing the structure of the fish community.

Our many speculative conclusions acknowledge the inconclusive nature of correlative evidence. This emphasizes the need for experimental field studies to further test hypotheses concerning the causal relationships underlying natural variations in species abundance. By intentionally changing lake trout density as suggested, the conformity of community response to hypothetical expectations could be effectively assessed. For example, lake trout density could be increased by stocking, to test whether smelt density would be further depressed, and whether recruitment of lake whitefish would increase with a parallel decline in the abundance of yellow perch. This approach assumes that lake trout are presently well below optimum density in the lake. Life history differences between lake trout and smelt, however, preclude very short-term regulation of smelt abundance (Stewart et al. 1983). Also, at some low density of smelt, lake trout would probably switch to a more profitable prey, limiting the extent to which smelt might be depressed.

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Abundance Patterns and Community Attributes of Fishes Relative to Environmental Gradients[1]

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Seventy-five lakes of the Canadian boreal forest were examined for patterns of fish species abundance and community structure in relation to gradients of four environmental variables: (1) lake area, (2) mean depth, (3) Secchi disk transparency, and (4) morphoedaphic index (MEI). Mean depth appeared to exert the greatest control on the relative abundance of the species considered. The remaining variables influenced abundance in unique ways, although, as with mean depth, this influence was mainly a consequence of changes in thermal and nutrient regimes. An examination of lower trophic components indicated that these regimes appear to structure food webs, with distinctly different patterns in food webs occurring in dimictic and polymictic lakes. Major shifts in aquatic biota occur in the transition region between lake types. Lakes with these characteristics are at a lower successional state due to environmental unpredictability, as demonstrated by an increasing importance of *r*- over *K*-strategists.

On a étudié 75 lacs de la forêt boréale canadienne pour la recherche de tendances de l'abondance des espèces de poisson et de la structure des communautés par rapport aux gradients de quatre variables environnementales : 1) superficie du lac, 2) profondeur moyenne, 3) transparence au disque de Secchi et 4) indice morphoédaphique. La profondeur moyenne semble être le paramètre qui exerçait la plus grande influence sur l'abondance relative des espèces étudiées. Les autres variables influaient sur l'abondance de façon particulière mais, comme dans le cas de la profondeur moyenne, cette influence résultait surtout de modifications du régime thermique et de celui des matières nutritives. Un examen des composantes trophiques inférieures a montré que ces régimes structuraient les réseaux alimentaires qui présentaient des allures très différentes dans les lacs dimictiques et polymictiques. Les principales modifications du biote aquatique, entre lacs de types différents, étaient notées dans la zone de transition. Les lacs présentant ces caractéristiques sont à un niveau évolutif inférieur à cause de facteurs environnementaux imprévisibles, comme le démontre la prédominance de plus en plus importante des stratégies *r* sur les stratégies *K*.

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Lakes situated on the Precambrian Shield are exceedingly numerous and variable in nature. Although many are near pristine, those close to population centers are being increasingly affected by an array of cultural stresses. Large and economically valuable lakes may be managed individually, but it is both financially and logistically impractical to attempt this for all lakes. Therefore, in Ontario, a typology of lakes based on the presence of particular fish assemblages has been developed to define groups of lakes for investigation and management (Ontario Ministry of Natural Resources 1978, 1982a, 1984).

While the occurrences of particular fish species are related to the environmental conditions of lakes (Stevenson et al. 1974; Johnson et al. 1977; Harvey 1978; Tonn and Magnuson 1982), the converse is not necessarily true. The presence of a species may be a temporary event in a model of colonization and extinction, while its absence may reflect the nature of the survey program or the occurrence of physiographic barriers to colonization, as with northern pike (*Esox lucius*) in the Algonquin highland area of southeastern Ontario (Johnson et al. 1977).

Hartmann (1980) described four fish community types in Europe based on the composition of fish yields and noted that the type of fish community present appeared to depend on the mean depth of the lake. Ryder and Kerr (1978) reported the occurrence of percid and salmonid communities in North American lakes. They described how the composition of fish communities varied with environmental conditions. They predicted that when fish communities were affected by exogenous stress (such as exploitation), the degree of persistence and integrity of these communities would be a function of environmental suitability.

Regier and Henderson (1973) proposed a general hierarchical model for the interaction of abiotic and biotic factors in determining the characteristics of fish production systems. Their goal was to identify the relationships between the usually studied characteristics of fish production systems (such as yield

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and composition) and the characteristics of ecological communities as elaborated by Margalef (1968). A synoptic survey of species abundance patterns, and community characteristics such as species diversity and community mean weight (average size of fish), would contribute to the development of these models (i.e. Regier and Henderson 1973; Ryder and Kerr 1978), and others.

The associations between species presence, abundance, or dominance, and environmental conditions are often identified through the application of multivariate ordination methods such as principal component analysis (e.g. Johnson et al. 1977; Harvey 1978). These techniques, however, assume linear models, while the response of a species along a single environmental gradient generally forms an "optimality" curve with densities declining (in a variable fashion) from a central optimum towards either end of the scale (Whittaker 1967). This nonlinearity causes a distortion, or "horseshoe effect" (Kendall 1975), in two-dimensional ordination space which may compound the interpretation of the axes and frequently produces misleading results (Austin and Noy-Meir 1971; Beals 1973; Austin 1976). Prior to such investigations, one should be aware of the degree of nonlinearity likely to be encountered. This implies knowledge of general patterns in the abundance of species across the range of each environmental variable considered.

Gradient analysis is a simple technique which is commonly used for such investigations within continuous environments (Whittaker 1967; Terborgh 1971). Conventionally, observations of the abundance of species and nature of species associations are made along transects which are interpreted to represent gradients of environmental conditions such as moisture content of soil. The observations are usually analysed by inspection of graphs of abundance against the environmental variable, and regions are identified where species dominate or patterns of community composition occur. It would be appropriate to consider a graded series of lakes as sites along a transect.

In this paper we use the technique of gradient analysis to describe the relationships between a number of fish community characteristics (relative abundance of species, species diversity, and community mean weight) and four environmental variables (lake mean depth, surface area, Secchi disk transparency, and morphoedaphic index (MEI)). The underlying factors responsible for these relationships are identified through an examination of environmentally induced changes in lower trophic components. We discuss how the composition and successional state of fish communities is related to food web structure and environmental variability. We offer recommendations for lake management in light of these analyses.

Methods

We examined a large number of published and unpublished reports and data summaries for information on gillnet catches and environmental characteristics for lakes of the Canadian boreal forest region. Seventy-five lakes were selected to embrace a wide range of environmental conditions and ensure a broad taxonomic representation of fishes. Only fairly remote and lightly fished lakes were included to avoid the confounding effects of anthropogenic stress in the analyses. With one exception, all lakes are located in northwestern Ontario (Fig. 1). Survey data were extracted from various sources. Pre-1972 lake inventories conducted by the Ontario Ministry of Natural Resources (OMNR) provided the required data for a group of 35 lakes. Unpublished data from intensive fisheries surveys of 26 lakes in the Patricia region (north of 51° latitude) of the province were also utilized. The remaining 13 Ontario lakes represent selected OMNR assessment and research lakes. Great Slave Lake, located in the Northwest Territories, was included to extend the range of lake size and depth. Fisheries data for this lake were collected prior to any major commercial fishing activity, as documented by Rawson (1951).

Lakes were usually sampled with standard net gangs ranging from 38 to 127-mm stretched mesh in increments of 12.7 mm. Some gear (e.g. that used in Great Slave Lake) departed slightly from this standard with some intermediate meshes omitted, but this was judged to have negligible bias on catch composition. Catch data for the Patricia Inventory lakes were adjusted to compensate for an uneven allotment of mesh per gang. Effort was relatively intensive and varied with lake size, ranging from four 91-m sets in the smaller lakes to 145 sets in Great Slave Lake. While gill nets are species and size selective (Moyle et al. 1950), we assume that the catch compositions for each lake represent indices of the number and relative abundance of species present and are comparable between lakes.

A total of 21 species were represented in the catches (Table 1). Catch data for all net sets were summed for each lake, and the abundance of each species was recorded as the percentage of total biomass and number. In a few cases, length data alone were available, and species weight (for biomass calculations) was then estimated from length utilizing regression equations developed from these and other northwestern Ontario lakes, or alternatively from equations reviewed by Carlander (1969, 1977). Mean weight was computed for each species, as was an overall "community mean weight" (CMW), representing the average size of all fish sampled from a given lake.

Three indices of species diversity were computed: (1) the number of taxa present (vulnerable to the gear), (2) the Shannon–Wiener function (Shannon and Weaver 1949; Pielou 1975), using the proportion of biomass belonging to each species, and (3) the index of community dominance (McNaughton 1968), defined as the percentage of biomass contributed by the two most abundant species.

Lakes were classified by two methods which reflect species abundance ratios, rather than the more common technique of clustering based on species presence and absence (Johnson et al. 1977; Harvey 1978). Our first method uses codominant species pairs to describe community configurations, with lakes grouped on the basis of the two species which contributed most to the catch (by weight). The second method uses terminal predator associations, with lakes grouped by the type and relative abundance of predatory fish (major game species) present.

Johnson et al. (1977), through discriminant analysis, identified lake area, mean depth, and Secchi disk transparency as limnological variables with the greatest utility in distinguishing fish associations in Ontario lakes. These three physical variables, along with MEI (Ryder 1965), were selected as key environmental variables for gradient analysis. Data were transformed to normalize their distributions, as determined by the Kolmogorov–Smirnov test (Sokal and Rohlf 1969). A square root transformation of Secchi depth was applied, while data for the other variables were converted to common logs. Table 2 identifies the mean and range of these variables. The presence or absence of stable thermal stratification was also recorded for each lake, as determined by inspection of depth profiles of water temperature.

Direct gradient analysis (as reviewed by Whittaker 1967) was

FIG. 1. Location of lakes in Ontario as represented by the stippled area of the map. Great Slave Lake is located approximately 1700 km to the northwest.

used to identify trends or patterns in the abundance of species, community groups, the information indices (species diversity and community mean weight), and the probability of thermal stratification along the four environmental gradients. Patterns were detected through visual and statistical inspections of gradient plots. Plots of species and community groups were created by aggregating data by classes of each environmental variable, with widths as follows: $\log_{10}$ mean depth − 0.2 units; $\log_{10}$ area − 0.5 units; $\log_{10}$ MEI − 0.25 units; square root Secchi depth − 0.25 units. Similar classes were used in plots of species diversity and CMW along each environmental gradient. CMW was plotted against the species diversity indices, with each index having the following class width: number of species − 1 species; Shannon-Wiener index − 0.25 units; community dominance index − 0.1 units.

Distributions of species, community groups, and the information indices were frequently normal across the entire gradient, but non-normal within environmental classes. Since we wished to compare means between classes of an environmental variable, it was logical to normalize at that level. Exact normalizing transformations can be computed from the expression $1 - b/2$, where b is the slope of the regression of variance on the mean (after $\log_{10}$ transformation) for a series of replicate samples (Taylor's Power Law, see Taylor 1961; Downing 1979). Accordingly, we used mean and variance data for depth classes to provide a data series from which to determine normalizing transformations. Catch percentages for walleye, northern pike, yellow perch, lake herring, and white sucker required conversion to common logs, while values for burbot and lake trout were raised to the power 0.25. Lake whitefish, the community groups, and the information indices did not require transformation.

Results

Patterns in Species Abundance

The seven highest-ranked of the 21 species vulnerable to the gear occurred in 30% or more of the lakes (Table 1). These

TABLE 1. Species occurrence and their rank (of contributed biomass) from 75 lakes. Species codes used in the illustrations are indicated.

Species	Code	Occurrence (no. of lakes)	Rank
Northern pike (*Esox lucius*)	NP	74	3
White sucker (*Catostomus commersoni*)	WS	73	1
Yellow perch (*Perca flavescens*)	YP	61	12
Walleye (*Stizostedion vitreum*)	WA	57	2
Lake whitefish (*Coregonus clupeaformis*)	LW	56	4
Lake herring (*Coregonus artedii*)	LH	50	6
Burbot (*Lota lota*)	B	33	7
Lake trout (*Salvelinus namaycush*)	LT	23	5
Shorthead redhorse sucker (*Moxostoma macrolepidotum*)		23	9
Longnose sucker (*Catostomus catostomus*)		18	8
Sauger (*Stizostedion canadense*)		16	10
Rock bass (*Ambloplites rupestris*)		9	18
Lake sturgeon (*Acipenser fulvescens*)		7	14
Goldeye (*Hiodon alosoides*)		6	11
Round whitefish (*Prosopium cylindraceum*)		6	16
Smallmouth bass (*Micropterus dolomieui*)		4	15
Mooneye (*Hiodon tergisus*)		3	13
Lake chub (*Couesius plumbeus*)		3	17
Brook trout (*Salvelinus fontinalis*)		2	19
Inconnu (*Stenodus leucichthys*)		1	20
Arctic grayling (*Thymallus arcticus*)		1	21

TABLE 2. Means and ranges of environmental variables selected for analyses.

Variable	Mean	Range
Lake area (ha)	1951	55–2 720 000
Mean depth (m)	5.1	0.9–62.0
Secchi disk transparency (m)	1.8	0.3–7.8
MEI	9.1	0.3–83.3

TABLE 3. Correlation matrix of environmental variables. A single asterisk indicates significance level $p < 0.05$; a double asterisk indicates $p < 0.01$.

	Area	Secchi depth	MEI
Mean depth	0.483**	0.778**	−0.878**
Area		0.291*	−0.220
Secchi depth			−0.741**

species, because of their relative importance, were selected for gradient analysis along with the near ubiquitous yellow perch. Zoogeographic studies (McPhail and Lindsey 1970) indicate that all eight species would likely have had access to these lakes at some point during the period of postglacial dispersion.

Figure 2 illustrates the response of these species to each environmental gradient. These plots represent relative abundances, defined as the percentage of the catch by weight contributed by each species within a single lake, and averaged over all lakes within each environmental class. Highlights are reported below, noting statistically significant differences ($p < 0.05$) as determined through *t*-tests which compared the means of adjacent groups.

Mean depth has a pronounced effect on all species (Fig. 2A). A depth of 6.3 m represents a key point[2] along the mean depth gradient. The peak in abundance for lake trout, burbot, and lake whitefish occurs in lakes of greater depth. Walleye, northern pike, white sucker, and yellow perch reach greater relative abundances in shallower lakes (<6.3 m), although walleye seldom occur in lakes of less than 1.6 m mean depth. The 6.3-m mean depth appears to represent most closely the point at which lakes that thermally stratify are separated from those that do not, which would explain the absence of lake trout in lakes of shallower depth. Lake herring tend to peak in abundance in lakes of intermediate depth (4–10 m).

Similarly, lake trout and burbot are virtually nonexistent in lakes less than 316 ha in area (Fig. 2B), and lake herring, lake whitefish, and walleye occur in lower relative abundances in such lakes. Conversely, northern pike and yellow perch peak in abundance in these small lakes. This dichotomy may to a degree reflect the occurrence of midsummer thermal stratification, as 93% of lakes less than 316 ha in area do not stratify, a phenomenon that apparently is a function of the strong correlation between lake area and mean depth (Table 3).

Abundance patterns attributable to water transparency are also discernable (Fig. 2C). An extreme peak in abundance of lake trout, and less obviously burbot and lake whitefish, occurs in lakes with Secchi depths greater than 4.0 m. Peaks in the concentration of walleye, northern pike, white sucker, and yellow perch occur in lakes characterized by lesser Secchi depths. The abundance of lake herring is low and fairly constant along the cline of water transparency, although slightly greater abundances are apparent in the least transparent lakes (0.25–0.56 m Secchi).

Along the MEI gradient (Fig. 2D), major shifts in abundances

[2]This depth, as with other "key" points identified along the environmental gradients, represents a boundary between two adjacent depth classes. As the classes were established arbitrarily, such key points represent approximations rather than the exact location along the gradient at which some event occurs.

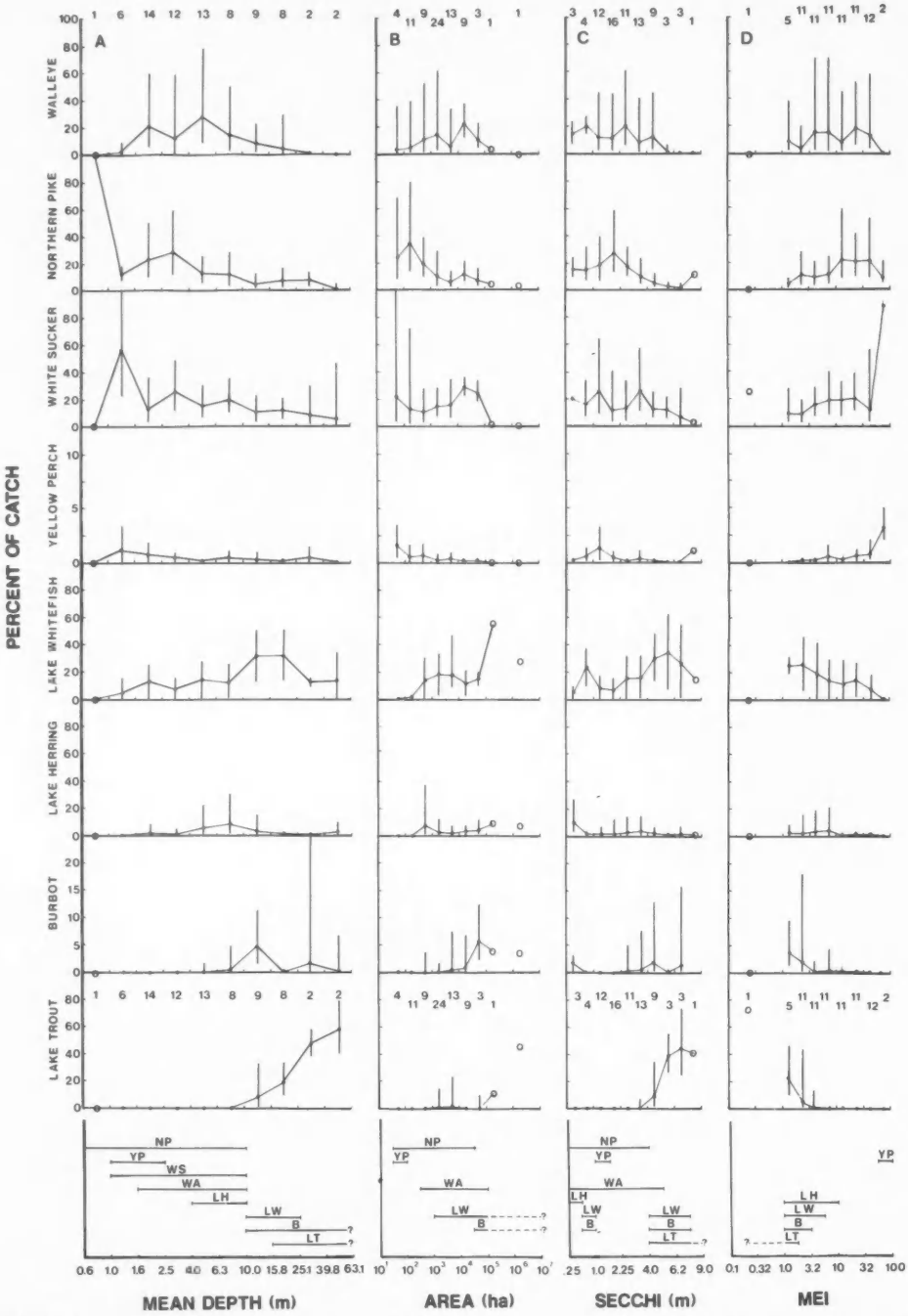

FIG. 2. Contribution (percent of catch by weight) of eight major fish species to gillnet catches from 75 lakes in relation to (A) mean depth, (B) lake area, (C) Secchi disk transparency, and (D) MEI. Each point represents the mean value for lakes contributing to successive classes of the environmental variables, while the vertical lines indicate ± 1 SD. The number of lakes in each class is noted along the top; open circles indicate single lakes. Note that the scale of the ordinate has been expanded to better illustrate the contribution of yellow perch and burbot. The bottom panel illustrates ranges of the environmental variables over which species contribute two thirds or greater of their maximum abundance. Abbreviated species names are defined in Table 1.

occur between the values 3.2 and 5.6. Lakes characterized by lower MEI values tend to have higher abundances of lake trout, burbot, and lake whitefish, with the abundance of these species decreasing dramatically (less so for lake whitefish) with higher values. The opposite pattern is apparent for white sucker, yellow perch, northern pike, and, to a lesser degree, walleye, with the former two species reaching peak abundances in the highest MEI class (56–100). The abundance of lake herring is relatively constant through the MEI range 1–10. As might be expected due to its depth component, MEI is predictive of thermal stratification, with all but 6% of lakes with MEI values less than 3.2 stratifying during the midsummer period.

The eight species dominating the biomass of these lakes may be separated into two major assemblages based on their response to different environmental conditions. Gradient analysis has demonstrated that the relative abundance of walleye, northern pike, white sucker, and yellow perch varies similarly along a set of environmental clines. These taxa form the nucleus of a harmonic percid community (Ryder and Kerr 1978). The remaining four species form the core of what might be termed a salmonid community (although lake herring in some respects span both groups). Lake whitefish, lake herring, and burbot are species most frequently occurring in lake trout lakes, if species belonging to the percid community are excluded (based on an inventory of 1633 Ontario lakes). These two major communities can be readily distinguished by their mirror image patterns of relative abundance in relation to the four environmental variables (Fig. 3A, 3B). The paired curves along each gradient would compliment each other perfectly but for the contribution of minor species not considered in the analysis.

Patterns in Species Diversity and Community Mean Weight

Three measures of diversity were computed. The number of species occurring in each lake (vulnerable to the range of mesh presented) ranged from 1 to 13, with on average 7 species captured. The Shannon–Wiener index, which is a function of both species number and their proportional abundances, has a negatively skewed distribution with a mean value of 1.9 and a range of 0–2.9. The index of community dominance measures the contribution of the two most abundant species to the total biomass, and hence is inversely related to the other measures of diversity. Community dominance is greater than 50% in all but six lakes, and exceeds 75% in one third of the cases. On average, 71% of the fish biomass is contributed by only two species.

Figures 3C–3E illustrate the distribution of values for these indices along the environmental gradients. The number of species is generally symmetric with the Shannon–Wiener index, while community dominance, as expected, forms a mirror image. Ranges in each variable have been identified which correspond to apparent peaks, troughs, or plateaus in each index, and their means have been tested for significant differences as indicated on each figure. Some of these differences require further discussion.

The parameter most highly correlated with species diversity is lake area, which displays a step-like pattern probably attributable to the area classes selected. The smaller lake classes (<316 ha) average only 3.5 species and exhibit low Shannon–Wiener values. Both indices increase sharply to the next step in lake size (316 – 10 000 ha) and then increase once more to peak in lakes near 100 000 ha. Community dominance displays the opposite trend, averaging 93% in lakes less than 316 ha and progressively less in the larger lake classes.

Significant positive correlations also exist between the diversity indices and mean depth, although in general, parabolic relationships are apparent. The number of species and Shannon–Wiener index are significantly greater when lakes exceed 6.3 m mean depth, while the opposite is true for community dominance. Each index demonstrates a highly irregular pattern along the Secchi depth gradient resembling a dampened sine wave. An obvious peak in diversity is associated with conditions of very low transparency (<1.0 m Secchi), a trough appears in the midrange (1.0–2.25 m Secchi), and a secondary peak occurs in more transparent waters. Only the Shannon–Wiener index demonstrates a significant (negative) correlation with MEI. However, all indices indicate that diversity is greater in lakes with MEI values than 10 than in higher MEI lakes.

CMW, the average weight of all species in the catch, ranged from 0.13 to 1.31 kg, with a mean value of 0.69 kg. Figure 3F illustrates patterns of CMW along the environmental gradients. Again, regions that differ significantly from adjacent zones are indicated on the figure.

Lake area is negatively correlated with CMW, with the reduction in size most obvious in lakes greater than 10 000 ha. Although not correlated with mean depth, CMW is at minimum in the 6.3–10.0 m class, where it averages 0.47 kg. Examination of the plot in relation to Fig. 3G reveals that 60% of lakes within this mean depth class are thermally stratified. The plot of CMW along the Secchi gradient somewhat resembles that of community dominance. A positive correlation is apparent, with significantly higher CMW values occurring in lakes exceeding 4.0 m Secchi depth. A depression in CMW occurs within the Secchi range 3.1–4.0 m, where again near 60% of lakes are stratified. Along the MEI gradient, the highest values of CMW occur when MEI is less than 5.6 (average 0.76 kg), are reduced somewhat through MEI classes 5.6–56 (average 0.67 kg), and are lowest when MEI exceeds 56 (average 0.29 kg). A depression in CMW occurs in the 5.6–10.0 MEI class where approximately 50% of lakes are stratified. It is apparent that minimum values of CMW observed along the gradients are associated with the transition between thermally stratified and unstratified lakes.

CMW and species diversity are negatively correlated, as illustrated in Fig. 4. Greater variation in CMW occurs, however, in lakes of low diversity. The decline in CMW is most pronounced when the number of species exceeds seven (Fig. 4A) or the Shannon–Wiener index exceeds 2.0 (Fig. 4B). The relationship between CMW and community dominance exhibits the greatest degree of linearity (Fig. 4C). CMW ranges from an average of 0.51 kg in lakes in which the two top-ranked species contribute less than 50% of the biomass to 0.92 kg when they constitute 100% of the catch.

Lake Classification Schemes

One method of lake classification was to type lakes based on codominant species pairs (the two most abundant species in the catch), which contribute on average 71% of the total biomass. Twenty possible combinations of species occurred. However, 88% of the lakes could be represented by 9 codominant pairs (Table 4); each of the remaining 11 pairs occurred in at most two lakes and were ignored.

Means and standard deviations of the four environmental

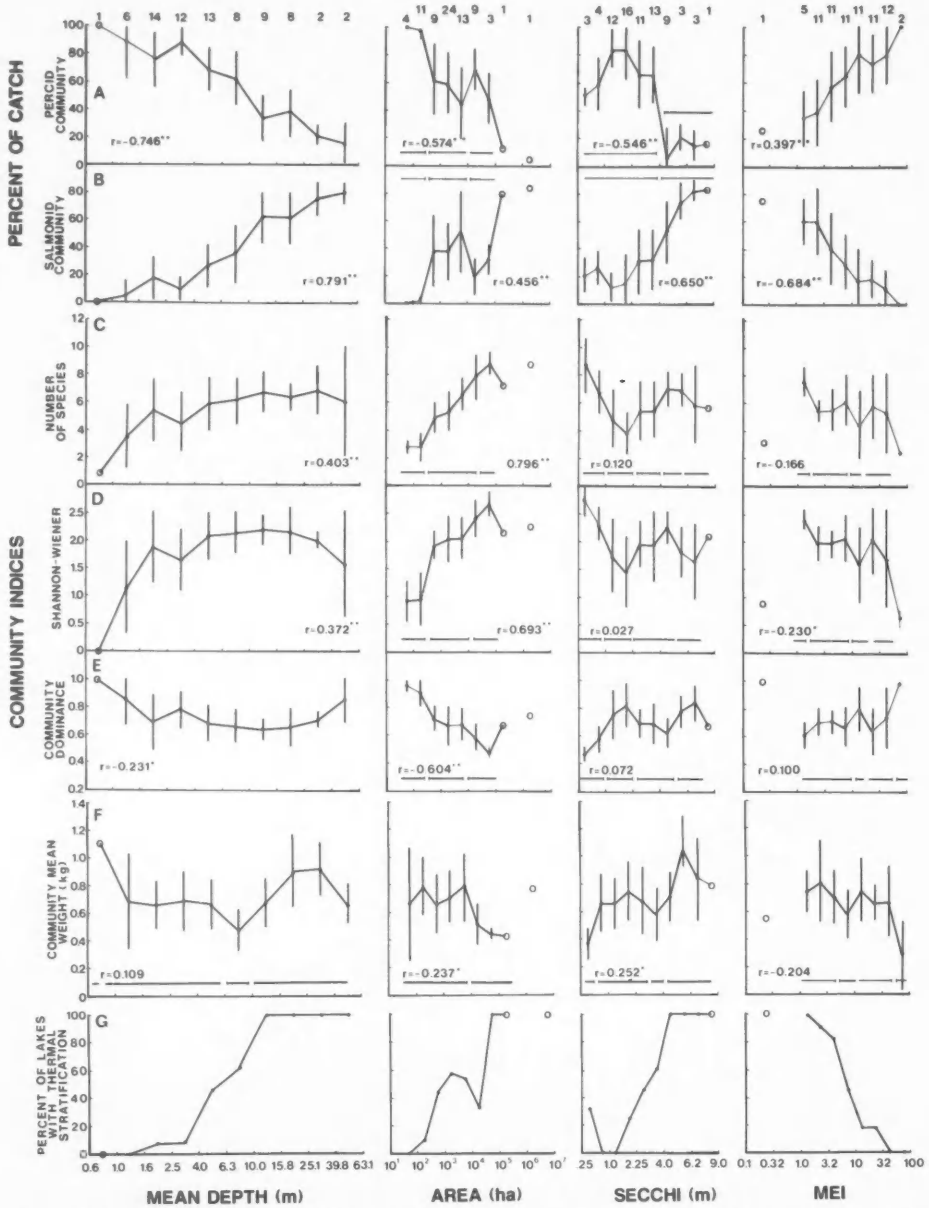

FIG. 3. Summed contribution (percent of catch by weight) of members of (A) the percid community and (B) the salmonid community (as defined in text) to gillnet catches from 75 lakes in relation to four environmental gradients. The community indices, (C) number of species, (D) Shannon–Wiener index, (E) community dominance, and (F) community mean weight are similarly illustrated along the gradients, as is (G) the percentage of lakes exhibiting stable thermal stratification. Each point represents the mean value for lakes contributing to successive classes of the environmental variables, while the vertical lines indicate ± 1 SD. The number of lakes in each class is noted along the top; open circles indicate single lakes. Horizontal lines on select figures illustrate regions selected for statistical comparisons by one-tailed *t*-tests. Vertical bars bounding these lines indicate a significant difference ($p < 0.05$) between means of adjacent zones, while the absence of bars indicates no difference between means. Correlation coefficients are included for each plot. A single asterisk indicates significance level $p < 0.05$; a double asterisk indicates $p < 0.01$.

variables were plotted along two-variable gradients for each of the nine lake types (Fig. 5). Lakes typed by the codominant pairs lake trout – lake whitefish or lake trout – white sucker have relatively greater mean depths and more transparent waters than the other seven lake types. With this exception, there was no significant difference between lakes classified according to codominant species along the four gradients (one-tailed *t*-tests; $p < 0.05$). However, the lake types appear to form three clusters

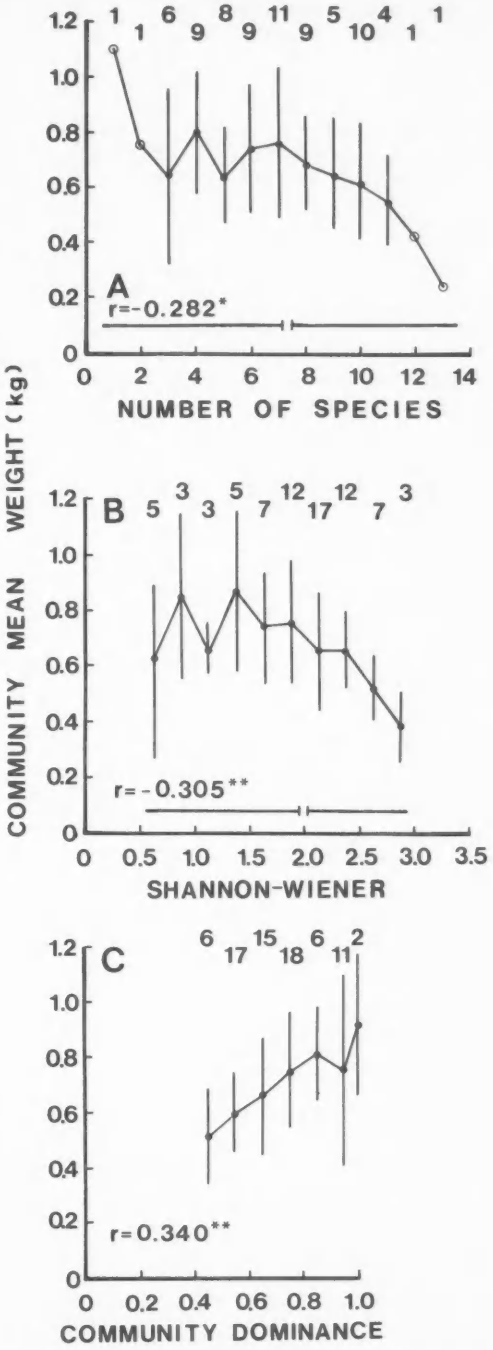

FIG. 4. Relationship between community mean weight and three diversity indices: (A) number of species, (B) Shannon–Wiener index, and (C) community dominance. Each point represents the mean value for lakes contributing to successive classes of the diversity indices, while the vertical lines indicate ± 1 SD. The last point on the community dominance plot represents the maximum value of 1.0 rather than a range. The number of lakes in each class is noted along the top of each figure; open circles indicate single lakes. Horizontal lines on select figures illustrate regions selected for statistical comparisons by one-tailed *t*-tests. Vertical bars bounding these lines indicate a significant difference ($p < 0.05$) between means of adjacent zones, while the absence of bars indicates no difference between means. Correlation coefficients are included for each plot. A single asterisk indicates significance level $p < 0.05$; a double asterisk indicates $p < 0.01$.

TABLE 4. Codominant pairs identified for lake classification and the percentage of lakes in which they occur.

Codominant species pair	% occurrence (all lakes)
White sucker – walleye	20
White sucker – northern pike	19
Walleye – northern pike	13
White sucker – lake whitefish	9
Lake whitefish – lake trout	8
Lake whitefish – walleye	7
Walleye – lake herring	5
White sucker – lake Trout	4
Lake whitefish – northern pike	3

TABLE 5. Terminal predator groups identified for lake classification and the percentage of lakes in which they occur.

Predators		% occurrence (all lakes)
Primary	Secondary	
Walleye	Northern pike	35
Northern pike	Walleye	24
Lake trout	Northern pike Walleye[a]	15
Walleye	Northern pike Lake trout	12
Northern pike	None	9

[a]Walleye not always present.

along the gradients, and the means of the environmental variables associated with each cluster do differ. Lakes in which northern pike occur, in combination with white sucker, walleye, or lake whitefish, form a cluster which identifies the smallest, shallowest, least transparent lakes with the highest MEI values. In contrast, a second cluster of lakes, characterized by lake trout paired with lake whitefish or white sucker, are large, deep, and clear, with low values of MEI. A third cluster is formed of lakes with codominant pairs of white sucker – walleye, white sucker – lake whitefish, lake whitefish – walleye, and walleye – lake herring. As a group, these lakes exhibit intermediate values of each environmental variable.

Our second classification scheme grouped lakes according to the occurrence and relative abundance of terminal predators. A total of 95% of the lakes were represented by one of the five groups identified in Table 5. Where northern pike or walleye occur as the dominant predator, predatory species contribute a near constant 50% of the total fish biomass (Table 6). This contribution is reduced to 41%, on average, in lakes in which lake trout dominate.

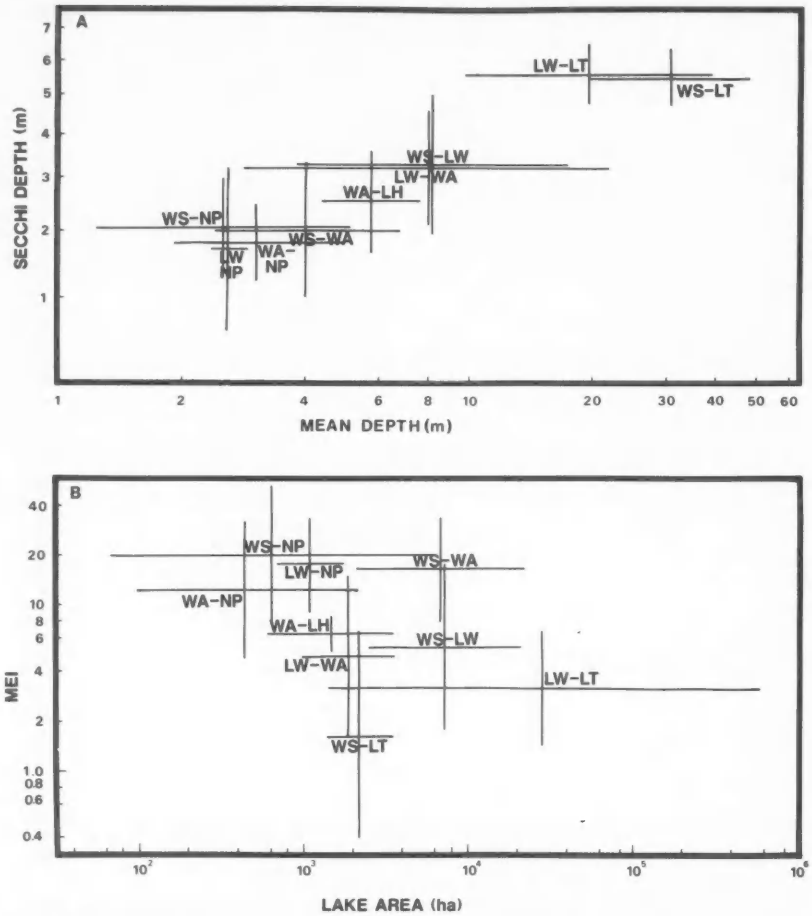

FIG. 5. Environmental conditions of lakes classed by codominant species. Each lake type is represented by its mean ± 1 SD along gradients of (A) Secchi disk transparency and mean depth and (B) MEI and lake area. Abbreviated species names are defined in Table 1.

The terminal predator associations clearly separate lakes along gradients of mean depth and lake area (Fig. 6). Northern pike frequently occur as the only predator in lakes both extremely shallow and small in area. The northern pike – walleye and walleye – northern pike combinations typify lakes of moderate depth and area. The terminal predator associations in which lake trout occur characterize the largest and by far the deepest lakes. All these differences are statistically significant ($p < 0.05$), as indicated by t-tests of adjacent groups.

Lakes with northern pike as the only predator do not differ statistically from those with other predator associations along a gradient of Secchi depth and MEI. However, the cluster of lakes with terminal predator combinations of northern pike, northern pike – walleye, or walleye – northern pike have significantly higher MEI values and lower Secchi depths than do lakes characterized by the other predator groups. Lakes in which lake trout represent the primary predator have greater Secchi depths than do lakes in which they are secondary to walleye and northern pike.

Discussion

Interpreting the Influence of the Environmental Variables

We have demonstrated that the relative abundance of species and the occurrence of particular community configurations are predictable along environmental gradients. To be truly meaningful, the underlying factors represented by each gradient must be identified. Such factors could be assessed by examining the influence of the environmental variable on major ecosystem characteristics. As lake mean depth has been shown to have a particularly dramatic effect on species abundance, and is most strongly correlated with the other three environmental variables, it is a logical variable to examine in this manner.

Mean depth of a lake is the primary physical variable controlling the thermal regime, that is, dictating the degree and duration of thermal stratification in a given set of climatic conditions (Straskraba 1980). In our lake set, lakes exceeding 10 m mean depth are typically dimictic, experiencing strong,

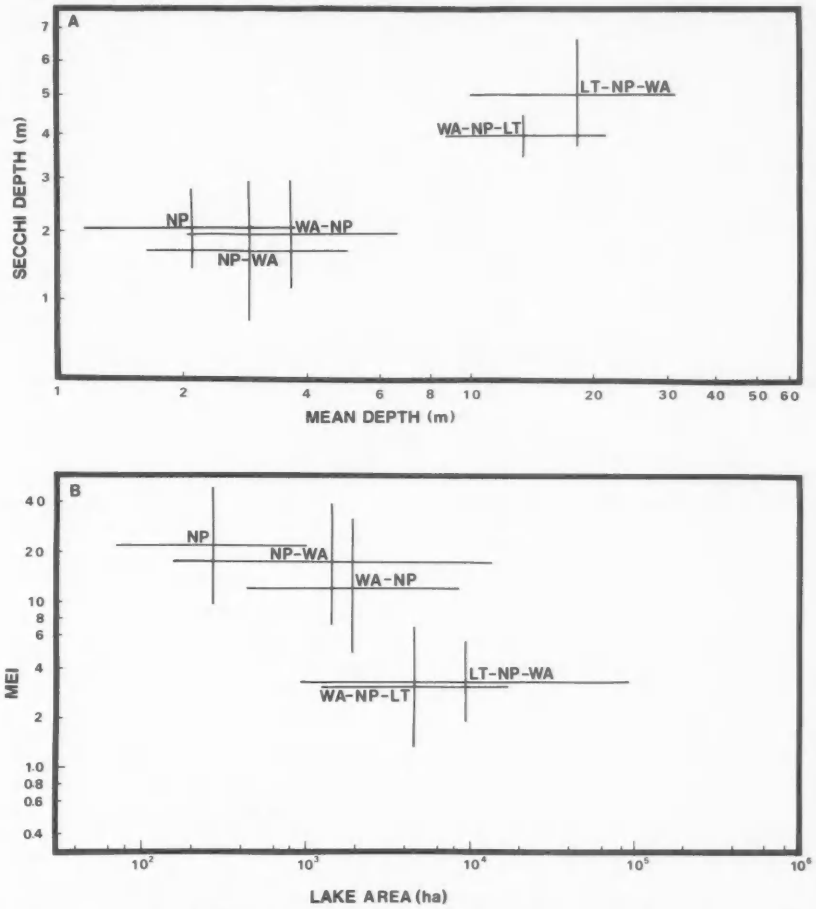

FIG. 6. Environmental conditions of lakes classed by terminal predator groups. Each group is represented by its mean ± 1 SD along gradients of (A) Secchi disk transparency and mean depth and (B) MEI and lake area. Abbreviated species names are defined in Table 1.

TABLE 6. Percentage of total biomass contributed by the various terminal predator groups.

Terminal predator group	Biomass	
	Individual contribution (%)	Group contribution (%)
Northern pike	50	50
Northern pike	31	
Walleye	17	48
Walleye	37	
Northern pike	14	51
Walleye	36	
Northern pike	13	
Lake trout	1	50
Lake trout	28	
Northern pike	6	
Walleye	7	41

stable thermal stratification. Those with mean depth less than 4 m may be termed "continuous cold polymictic" (after the classification of Lewis (1983)), as they usually mix daily throughout the open-water season. Lakes of intermediate mean depth (4–10 m) may fit either of the above categories, but most frequently are of the "discontinuous cold polymictic" type (Lewis 1983). Such lakes stratify for short, irregular periods throughout the summer, interrupted by mixing.

Phosphorus is the key nutrient controlling primary production and phytoplankton standing stock in lakes (Schindler 1978). Sakamoto (1966) described an overall negative hyperbolic relationship between the total phosphorus concentration and lake mean depth. Sakamoto's shallower lakes did not fit this pattern, however. Phosphorus tended to increase with mean depth up to approximately 5 m, after which it demonstrated a hyperbolic decline. Peak nutrient concentrations should therefore occur in the deeper unstratified lakes. Seasonal changes in nutrient concentrations also differ with lake type, as summer phosphorus concentrations exceed that of the spring or fall period in shallow eutrophic lakes, while the converse is true in dimictic lakes (Sakamoto 1966; Prepas and Trew 1983).

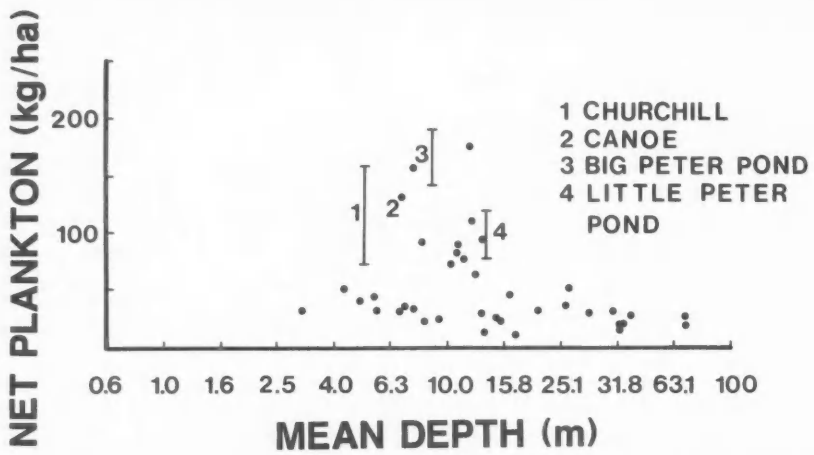

FIG. 7. Relationship between lake mean depth and the standing crop of net plankton for boreal forest lakes of Saskatchewan. Sources for data were Rawson (1955, 1957, 1060a, 1960b), Mendis (1956), Ruggles (1959), Koshinsky (1964, 1965), and Johnson (1971). Vertical lines represent ranges of values for net plankton sampled over different years.

The concentration of chlorophyll in the euphotic zone has long been used as an index of phytoplankton standing crop, although the accuracy of its representation is uncertain (Nicholls and Dillon 1978). Sakamoto (1966) noted that chlorophyll content is low in shallow lakes with luxuriant growth of macrophytes, but tremendous blooms of phytoplankton occur if macrophytes are absent, explaining this as an antagonistic relationship between the two groups. This is supported by Landers' (1982) study of an Indiana reservoir in which phytoplankton and periphyton chlorophyll *a* increased markedly in response to the senescence (and subsequent nutrient release through decomposition) of large stands of *Myriophyllum spicatum*. Westlake (1980) found that the relative contributions of macrophytes and phytoplankton to primary production could not be deduced from current studies, but suggested that an increase in lake mean depth should increase the importance of phytoplankton, while the reverse should favour periphyton and macrophytes. He also stated (citing Spence 1976) that increases in nutrient levels would favour dominance by phytoplankton due to their shading effect. Chambers and Kalff (1985) have demonstrated that the depth of macrophyte colonization is highly correlated with Secchi depth.

Both Sakamoto (1966) and Oglesby (1977a) found chlorophyll concentrations to be negatively related to mean depth in a hyperbolic fashion. However, if Sakamoto's data for shallow lakes are considered, a pattern emerges similar to that of phosphorus, with an increase in chlorophyll concentrations to a peak in the vicinity of 5 m mean depth and then a decline. This is predictable from the strong correlations described between phosphorus and chlorophyll (Nicholls and Dillon 1978; Schindler 1978).

Net plankton consists of seston particles 60 μm or larger (depending on mesh used), which largely represent zooplankton although some algae and nonliving material are included (Rawson 1953). An examination of numerous lakes covering a wide range of mean depth reveals that a large fraction of lakes from the 4.0–15.8 m depth range have relatively higher standing crops of net plankton than the remainder (Fig. 7). A decline in biomass of net plankton occurs in lakes less than 6.3 m mean depth and then again in much deeper lakes. This curvilinear pattern may be the reason Patalas (1971) reported a positive correlation between zooplankton abundance and maximum depth, while others (Rawson 1953; Hanson and Peters 1984) observed a negative correlation. Patalas (1971) included numerous small, shallow lakes in his analysis, and his data probably describe the ascending limb of the abundance–depth curve, while the other two studies may describe the pattern of decreasing abundance occurring at greater depths.

Brylinsky (1980) examined correlations between abiotic variables and the annual production of zooplankton and benthos. He observed that factors having a positive correlation with zooplankton usually had a negative correlation with benthos, and vice versa, leading him to suggest that these two groups indirectly compete with each other. Rawson (1955) described the familiar hyperbolic relationship between lake mean depth and benthos biomass. However, Hayes (1957) was unable to detect any direct relationship between benthos standing stock and mean depth from a larger set of European and North American lakes. He described the distribution of observations as W-shaped (Fig. 8A). We have compiled and plotted benthos biomass data from various Canadian sources (Fig. 8B–8D) which demonstrate patterns congruent to that described by Hayes (1957). Although slight shifts in the "W" occur, there is an obvious biomass minimum for benthos in the 4–10 m mean depth range, which overlaps the apparent peak in biomass of net plankton.

This minimum may be a consequence of seasonally unfavourable concentrations of dissolved oxygen in the deeper waters. Hamilton's (1971) data from the Experimental Lakes Area (ELA) of northwestern Ontario reveal that lakes with low standing stocks of benthos also exhibited low oxygen concentrations in the deeper waters. Britt (1955) reported large numbers of head *Hexagenia* following a short period of stratification and oxygen depletion in the western basin of Lake Erie. The abundance and distribution of benthos were controlled by oxygen concentrations and temperature in El Capitan reservoir

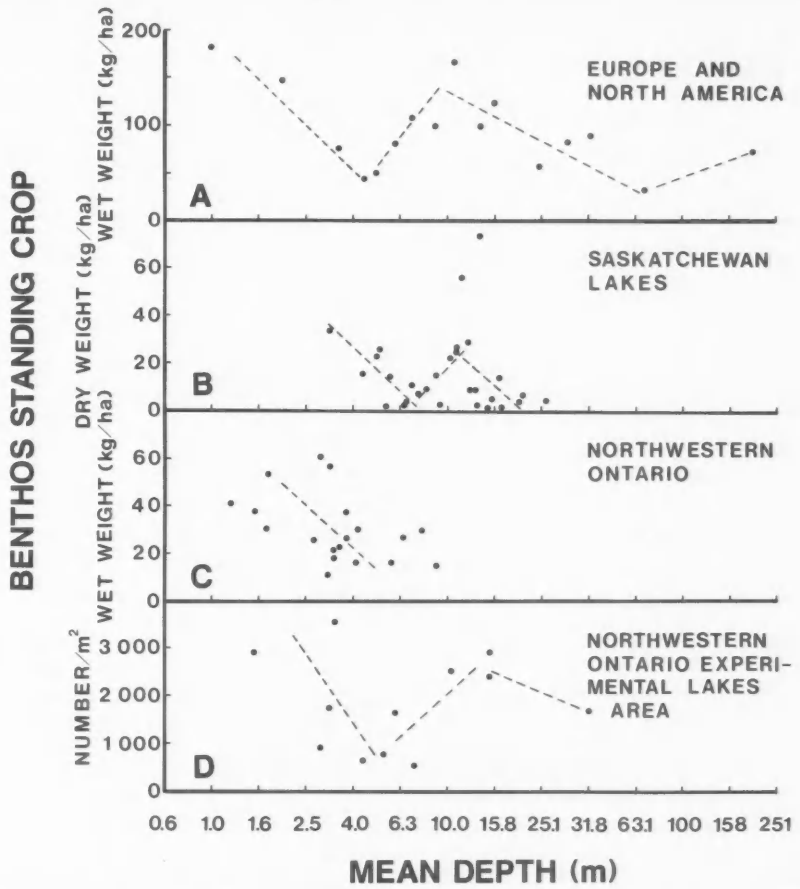

FIG. 8. Relationship between lake mean depth and benthos standing crop. Separate plots were required because of differences in collection methods and units of measurement. Trend lines have been drawn by eye. Sources for data were (A) Hayes (1957), (B) as listed for Fig. 7, (C) Cullis (1986), and (D) Hamilton (1971).

in California (as reviewed by Brinkhurst 1974). Chironomids normally did not occur at depths greater than 10 m, but following destratification and oxygenation through aeration of the hypolimnion, they were found at all depths and, along with oligochaetes, increased in abundance.

There is an obvious succession of benthic taxa in relation to mean depth of Ontario lakes (Fig. 9). Dipterans dominate the numerical composition in shallow lakes, while sphaeriid clams and amphipods dominate the benthos of deeper lakes. In ELA lakes, these amphipods were primarily *Pontoporeia hoyi* (Hamilton 1971). This species, together with sphaeriid clams and *Mysis relicta*, is a major and often dominant component of the profundal benthos of oligotrophic lakes (Rawson 1960a; Cook and Johnson 1974). The transition between the dipteran-dominated benthos of shallow lakes and the oligotrophic species appears to occur over the depth range 6.3–10.0 m.

These changes in the food web, together with temperature considerations, visually correlate with shifts in fish species abundance along a gradient of mean depth. A percid (cool-water) community is predominant in polymictic lakes shallower than 6.3 m mean depth. Conversely, a salmonid (cold-water) community is predominant in lakes which display stable thermal stratification (>10.0 m mean depth). Planktivorous lake herring reach their peak abundance at an intermediate mean depth, which overlaps the zone of highest zooplankton abundance and low benthos biomass, and signifies the dominance of pelagic or semipelagic food webs.

Changes in ecosystem characteristics along a continuum of lakes arranged by mean depth have been summarized (Table 7). Gradients of lake area, MEI, or Secchi depth would be expected to describe a similar series of changes through their correlation with mean depth, but would also contribute unique information. Lake area alters the mixing characteristics, hence the thermal regime, of lakes (through fetch) which has major effects on the biotic components (Straskraba 1980). Lake area also serves to index the array of habitats available in lakes, as does mean depth (Ryder et al. 1974). Ecosystem characteristics explained by MEI would be similar to that of mean depth, but MEI would better reflect nutrient concentrations and hence deepwater oxygen conditions. Secchi disk transparency describes light

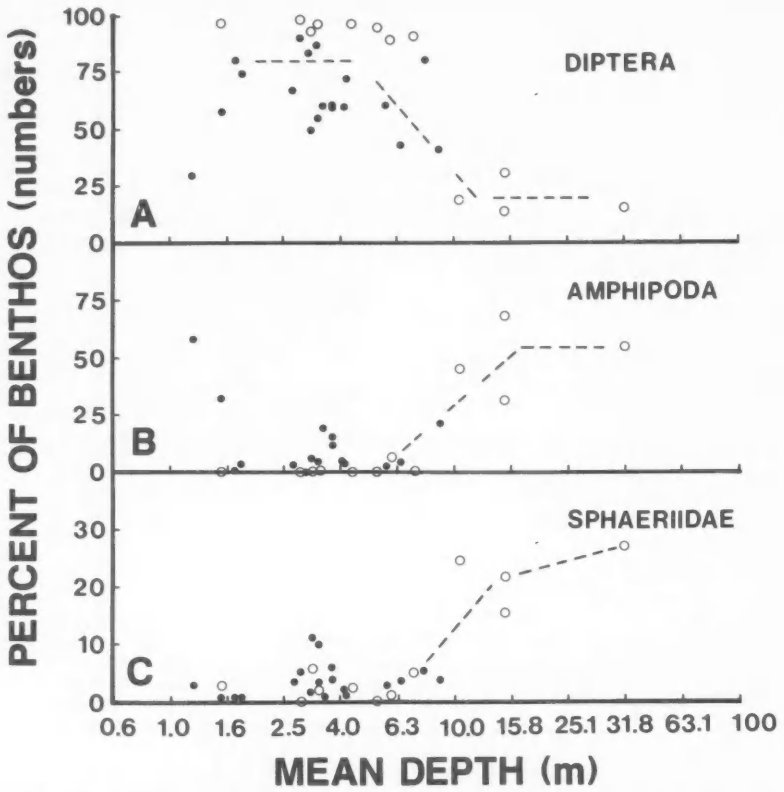

FIG. 9. Relationship between lake mean depth and the relative numeric abundance of three taxonomic groups of benthos from northwestern Ontario lakes. Trend lines have been drawn by eye. Note that the ordinate scales differ. Sources for data were Hamilton (1971) (open circles) and Cullis (1986) (closed circles).

TABLE 7. Select abiotic and biotic characteristics of three depth classes of boreal forest lakes. Class boundaries may vary as the thermal regime is modified by lake orientation, fetch, flushing rate, latitude, altitude, etc.

Characteristic	Mean depth		
	<4 m	4–10 m	>10 m
Thermal regime	Continuous cold polymictic	Discontinuous cold polymictic	Dimictic
Bottom O_2 concentration	High	Low if stratified, otherwise high	High
Nutrient levels	Low if macrophyte dominated, otherwise high	Intermediate if stratified, otherwise high	Low
Chlorophyll *a* concentration	As for nutrient levels	As for nutrient levels	As for nutrient levels
Zooplankton biomass	Low	High	Low
Benthos biomass	High	Low	High
Dominant benthic components	Diptera	Mixed	*Pontoporeia* *Mysis* Sphaeriidae
Fish community	Percid	Mixed	Salmonid
Lake herring abundance	Low	High	Low
Community mean weight	High	Low	High

attenuation by colour and turbidity, one component of which is phytoplankton (Brezonik 1978). Overall, we suspect that the variables selected for gradient analysis primarily serve to index the thermal and nutrient regimes of lakes. Given this, the general structure of the food web is defined in terms of the relative abundance of macrophytes and phytoplankton, and of benthos and zooplankton.

Ryder et al. (1981) described the major elements of fish production systems and their linkages. Chronologically, with respect to the colonization of species, these are as follows. Firstly, environmental conditions must fall within the physiologically survivable limits of the species, as defined by genotype. Secondly, an array of resources (forage, spawning areas, etc.) must be present and available (considering competition), within the range of phenotypic expression for the species. Thirdly, the species must be able to reproduce at a rate to balance predation and other mortality forms.

This summary is a considerable oversimplification of the natural processes outlined by Ryder et al. (1981), but serves to isolate the influence of abiotic environmental characteristics on the presence and relative abundance of species. Beyond this, species abundance is being shaped by successively more complicated interactions (i.e. competition and predation) with other components of the food web. We consider that our gradient plots report the average results from the interaction of all factors influencing food web characteristics.

Species Diversity, Community Mean Weight, and Ecological Succession

The process of ecological succession culminates in a biotic community which is at a maximum of biomass, information content, and symbiotic function, while exhibiting slow turnover (Margalef 1968; Odum 1969). The extent to which succession can proceed is limited by the predictability of environmental conditions (Margalef 1967, 1968). We can both detect and predict environmental conditions under which succession is constrained by abiotic environmental predictability.

In lakes experiencing summerkill and winterkill, succession is reversed through mortality of fish populations. Lakes with a high probability of winterkill can be identified on the basis of mean depth and MEI (Ryder et al. 1974). The usual factors resulting in fish kills are adverse conditions of temperature, hydrogen sulfide, and (most importantly) dissolved oxygen, acting singly or in combination (Greenbank 1945; Patriarche and Merna 1970). The phenomenon of oxygen depletion is a function of initial oxygen reserves, sediment and water column oxygen demands (as related to primary production), and the time period before photosynthesis or mixing renews oxygen levels (Cornett and Rigler 1979; Mathias and Barica 1980). Given the importance of water column storage, we expect that shallow dimictic lakes would have the greatest risk of summerkill and polymictic lakes (shallower still) would have the greatest risk of winterkill.

Nutrients are recycled during the summer in polymictic lakes (Sakamoto 1966; Prepas and Trew 1983). By definition, this recycling would be pulsed in discontinuous polymictic lakes. This is an example of environmental unpredictability in this lake type, which contrasts with the relatively steady seasonal decline in epilimnetic nutrients in lakes with stable thermal stratification. The pulsing of nutrients causes blooms of phytoplankton; hence, phytoplankton biomass tends to be an unpredictable component of the food web. Margalef (1967) observed that the occurrence of algal blooms in eutrophic lakes is a definite indicator of low diversity in phytoplankton and implies an early successional stage.

CMW is considered to be inversely related to the P/B ratio for larger members of the fish community (based on the size spectrum model of Kerr (1974) and the r_m:body size model of Fenchel (1974)). CMW is minimal in discontinuous polymictic lakes. The implied high P/B ratio and low CMW indicate that these systems are comparatively less mature and that r-strategy is being favoured. Lake herring are examples of such strategists and reach peak relative abundance within this lake type.

Species diversity is a function of the range of resources and how they are partitioned (realized niches) among the species present. Stability, in the sense of regulation (Regier and Henderson 1973), is thought to be positively correlated with diversity (Margalef 1968), leading some investigators to recommend its use as an index of fish community health (Regier and Loftus 1972; Regier and Henderson 1973). Our measurements of diversity provide an initial scaling of this index and an opportunity to evaluate its performance by comparison with other indices. There is no difference between the Shannon–Wiener index values for discontinuous polymictic and dimictic lakes. CMW is positively correlated with the community dominance index and negatively correlated with the number of species and Shannon–Wiener index (Fig. 4). This indicates that diversity is lower in more mature systems.

Margalef (1968) suggested that in some ecosystems, diversity initially increases during succession and then declines. The "intermediate disturbance hypothesis" of Connell (1978) describes a gradual increase in diversity to a maximum at some intermediate level of disturbance, followed by a decline. The high diversity at intermediate disturbance levels is maintained because resources are not limiting. At low levels of disturbance, competitive exclusion occurs, while at high levels, few species can tolerate the disturbance. The model was developed to explain diversity observations for trees in tropical rain forests and coral on tropical reefs. It has since been verified by a study of benthos in relation to fish grazing on coral reefs (Hixon and Brostoff 1981).

The phenomenon of metaphoetesis (Hutchinson 1959; Kerr 1979) may also play a role in explaining diversity patterns. Large species such as the top predators pass through a number of growth stanzas with associated diet changes during their life history (for examples, see Scott and Crossman 1973). The realized niche of such species is comparatively large in terms of the range of resources used (e.g. size of prey); hence, an environment can support fewer species than it could if feeding niche breadths were smaller (Schoener 1974).

This phenomenon affects our interpretation of diversity indices, effectively causing underestimations of diversity in lakes dominated by K-strategists, since they display the greatest degree of metaphoetesis. The change in the relationship between CMW and diversity (at a Shannon–Wiener value of 2) can be considered to represent a change in the strength of forces structuring fish communities. All things being equal, the negative correlation of CMW and diversity indicates a decline in dominance of relative K-strategists and an increase in importance of r-strategists, with increasing diversity.

We choose the intermediate disturbance hypothesis as being the most likely explanation for the change in the CMW–diversity relationship. We suggest that disturbance (in terms of

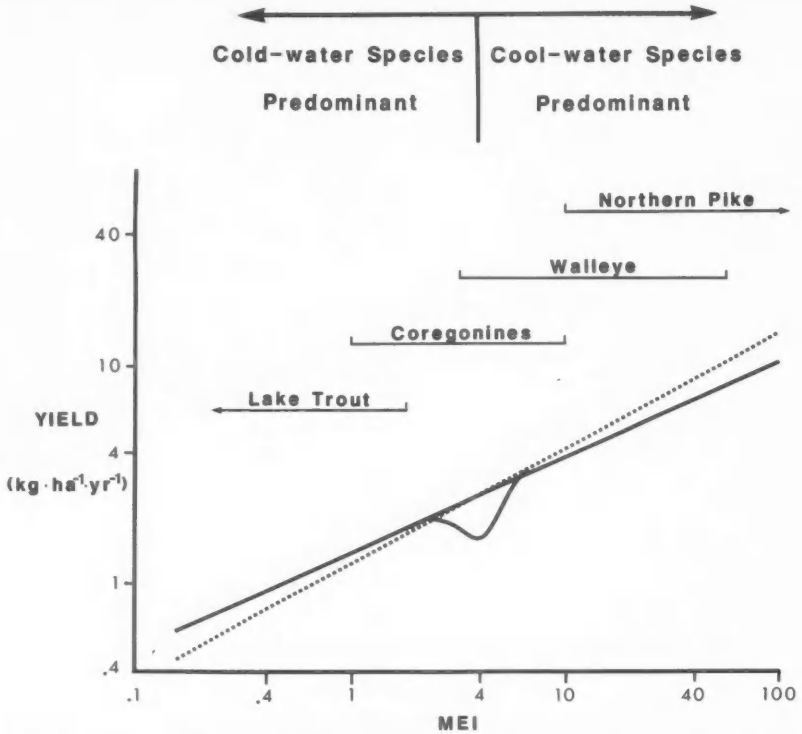

FIG. 10. Regressions of total fish yield on MEI, using equations of Ryder (1965) (solid line) and Matuszek (1978) (broken line). In thermally stratified lakes, we anticipate a reduced or variable yield at the point of maximum overlap between salmonid (cold-water) and percid (cool-water) dominated communities, as illustrated by the trough in the regression line near MEI 4.0. The horizontal bars indicate the MEI range over which commercial species maintain their greatest relative abundance.

biotic/abiotic unpredictability) is relatively more important in structuring fish communities which have Shannon–Wiener values exceeding 2.

Management Implications

Tonn et al. (1983) suggested multivariate community analysis be applied as a management technique to identify fish assemblages and the environmental factors responsible for their maintenance. Our gradient analysis contributes toward such an approach by providing a qualitative and quantitative description of the fish community of lentic ecosystems across a range of environmental variables.

Possible shifts in species dominance resulting from anthropogenic influence may be anticipated by examining the usual abundance of individual or codominant species in relation to the abiotic characteristics of the lake in question. Lake whitefish in Whitefish Lake, for example, have declined in abundance to near extinction following the introduction of walleye (P. A. Ryan, unpubl. data), a phenomenon that has also been observed in some of the Kawartha lakes (Lewies 1976). The observed shift in dominance from lake whitefish – northern pike to walleye – northern pike in Whitefish Lake is not unexpected, considering that these codominant groups typify environmentally similar lakes (Fig. 5).

As a group, terminal predators appear to contribute a near constant 50% of the total fish biomass, or slightly less when lake trout dominate. Such system conservatism would predict future states in an ecosystem undergoing change. Walleye are currently being introduced into many lakes in northern Ontario in which northern pike have historically occurred as the only predator. As walleye gain in abundance, a corresponding reduction in northern pike could be expected to maintain the predator balance near the 50% level. An indication as to the ultimate ratio of species once an equilibrium is reached may be inferred through an inspection of species abundance patterns along the environmental gradients (Fig. 2) and an examination of the lake's position on the terminal predator plots (Fig. 6).

Energy transfer efficiencies vary considerably between lakes, and the reasons for this are not entirely understood (Oglesby 1977b). Environmental unpredictability is an important characteristic of reservoirs (Ryder 1978) and defines winterkill lakes (Ryder et al. 1974). We anticipate that transfer efficiencies would be reduced through environmental unpredictability. The theme should be further explored, possibly in terms of lake flushing rates as they may define a position on the continuum between lentic and lotic systems based on the ratio of autochthonous to allochthonous production (Ryder and Pesendorfer 1988).

Total fish yield should reflect differences in transfer efficien-

cies, and composition of yield should reflect community structure along the environmental gradients that we have described. Colby et al. (1972) hypothesized that with an increase in MEI, shifts would occur in the taxonomic makeup of the fish community concurrent with an increase in total fish yield. They suggested that along a gradient of MEI (representing an index of lake trophic status), dominant species would sequence from salmonines to coregonines to percids and finally to esocids. We have demonstrated that such events do occur as suggested (Fig. 2), with lake trout yielding in dominance to lake whitefish, then walleye, and then northern pike as MEI increases through the range 0.3–83. There is an apparent shift from a fish community dominated by cold-water species to one of cool-water species occurring at about MEI 3–5 (Fig. 10). Members of the percid group are usually predominant in lakes with greater MEI values and members of the salmonid group are predominant at lower values, with lake trout reaching maximum relative abundances in the smallest MEI classes.

As MEI values increase through the range 3–5, major environmental changes would be expected in dimictic lakes, with an increase in the rate of organic sedimentation and a reduction in mid- to late-summer hypolimnetic oxygen concentrations. In general, oxygen deficits would occur in all stratified lakes of this MEI range (or greater) regardless of their depth. In shallow lakes, this would be a consequence of their inherent small hypolimnetic thickness, hence low oxygen reserves. In deeper lakes, an increased nutrient pool resulting in higher levels of primary production would be responsible for the deficits.

The MEI range 3–5 appears to identify the shift from more oligotrophic to more mesotrophic environments and would correspond to the zone of overlap between Ryder and Kerr's (1978) harmonic salmonid and harmonic percid community. They associated astatic aggregations of species with this overlap zone and suggested that such fish communities would exhibit low levels of persistence and variable levels of integrity. CMW is low in such lakes. This would indicate relatively less mature systems and a favouring of *r*- over *K*-strategists, hence the dominance of coregonines (largely lake herring) in this MEI region. Somewhat lower total fish yields might be expected from these stratified lakes (Fig. 10) as a consequence of lower transfer efficiencies associated with such an unpredictable environment. Lakes within this MEI region are not well represented in empirical yield prediction models (e.g. Ryder 1965; Matuszek 1978). Such lakes appear to be less capable of supporting long-term intensive fisheries, which was a data selection criterion in the development of these models. Collection of additional yield–MEI data is required to substantiate this effect and may uncover further depressions in the yield curve associated with environmental unpredictability and community transition.

A biotic indicator system (Ryder and Edwards 1985) may be used to type lake ecosystems, since the presence and abundance of indicator organisms integrate year-round environmental information. A ratio to describe benthos such as chironomid: *Pontoporeia* abundance may be valuable in this regard. Similarly, the description of fish community characteristics along major environmental gradients suggests classification schemes for lakes. The boundaries we describe, however, reflect both the correlations between the environmental variables and our choice of intervals for plotting. Caution should be exercised in transporting these empirical models, as regional and climatic influences may affect these intercorrelations and differences in fauna may affect species interrelationships.

For management purposes, lakes in Ontario have been typed based on the presence or absence of six species of fish (Ontario Ministry of Natural Resources 1982a). Studies of a representative sample of lakes have been undertaken to develop an understanding of the fish community dynamics of each lake type and thereby improve strategies for management (Ontario Ministry of Natural Resources 1984). It is expected that lakes which have similar fish community characteristics should react similarly to various types and levels of anthropogenic stresses, such as fishing and water-level regulation. This assumption could be strengthened if lakes grouped for comparative analysis or management purposes were environmentally similar. Our scaling of the influence of environmental variables provides an appropriate starting point for environmental classification, and at least partially addresses related questions, such as the possible ecological significance of a difference in mean depth between lakes.

Environmental classification may have a number of related applications. In Minnesota, fisheries managers regularly compare indices of fish abundance (gillnet and trapnet catch per unit of effort) with regional and statewide indices (Moyle et al. 1950). The accuracy of conclusions derived may be improved by restricting the comparisons to environmentally similar lakes. Environmental classification may also assist in the prediction of fish yield composition. The partitioning of yield among species has been described for Ontario lakes largely on the basis of catch averages for particular community types (Ontario Ministry of Natural Resources 1982b). Our observations, and those of Hartmann (1980) for European lakes, suggest that a description of yield composition which also takes into consideration lake environmental types may refine predictions of this sort.

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Perch (*Perca fluviatilis*) and Pike (*Esox lucius*) in Windermere from 1940 to 1985; Studies in Population Dynamics

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Le Cren, E. D. 1987. Perch (*Perca fluviatilis*) and pike (*Esox lucius*) in Windermere from 1940 to 1985: studies in population dynamics. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 216–228.

The adult population of perch (*Perca fluviatilis*) in Windermere was severely reduced by an experimental trap fishery from 1941 to 1947 in one basin and from 1941 to 1964 in the other and has been monitored since. A gillnet fishery for pike (*Esox lucius*) >550 mm began in 1944 and has continued since. Changes in numbers, recruitment, mortality, growth, biomass, and fecundity have been measured. Summer water temperature and population density affected perch growth; temperature affected pike growth from 1944 to 1959, but not thereafter. A model involving correlations with temperature and negative correlations with abundance of adult perch and 0 group pike explained 90% of variation in perch recruitment for part of the period. Pike recruitment was correlated with temperature. In perch adult mortality rate and growth rate are correlated. Perch numbers are recovering after a 98% adult mortality from disease in 1976. Temperature and size-related predation within and between the two species appear to be the main controlling factors, but the relationships have changed from one part of the period to another.

La pêche expérimentale à la trappe, menée de 1941 à 1947 dans un bassin du lac Windermere et de 1941 à 1964 dans l'autre bassin, a entraîné un déclin marqué de la population adulte de perche (*Perca fluviatilis*) qui, depuis, fait l'objet d'un contrôle. La pêche du brochet (*Esox lucius*) de longueur >550 mm au filet maillant a lieu depuis 1944. On a quantifié les variations du nombre, du recrutement, de la mortalité, de la croissance, de la biomasse et de la fécondité. La température de l'eau en été et la densité des poissons ont influé sur la croissance de la perche tandis que la température a influé sur la croissance du brochet de 1944 à 1959. Un modèle portant sur les corrélations avec la température et les corrélations négatives avec l'abondance de perche adultes et de brochets d'age 0 explique 90 % de la variation du recrutement de perche pendant une certaine partie de cette période. Le recrutement de brochet était corrélé avec la température tandis que chez la perche adulte, les taux de mortalité et de croissance étaient en corrélation. L'abondance de perche se rétablit après une mortalité massive, liée à la maladie, de 98 % des adultes en 1976. La température et la prédation intra-spécifique et inter-spécifique liée à la taille semblent être les principaux facteurs limitatifs, mais les relations ont changé d'une partie de la période à l'autre.

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At the start of the Second World War, Worthington (1950) initiated experimental fisheries on Windermere with three aims: (a) to demonstrate that British lakes could be cropped for human food in wartime, (b) to improve sport fisheries for salmonids by reducing the abundance of perch (*Perca fluviatilis*) (a competitor) and pike (*Esox lucius*) (a predator), and (c) to carry out an experiment on fish populations that might illuminate the "overfishing problem."

The information gained from studies of the effects of this experimental manipulation of fish populations and natural fluctuations has become the major product of the project and has resulted in its continuation until beyond 1985.

The present paper is a brief summary of the studies on perch and pike and a discussion of the contribution they may make to the general understanding of fish population dynamics. Previous papers have presented detailed accounts of aspects of particular periods and particular species, background information, and studies to develop and authenticate methodology; I shall report on them only to the extent necessary for an understanding of the principal conclusions. These are, essentially, the abiotic and density-dependent factors controlling growth, recruitment, mortality, and the relationships between the two species.

Background Information

Windermere

Windermere is an elongated lake lying in a glacially deepened valley in northwest England. It has a total area of 14.8 km^2 and is divided by islands and shallows into two basins designated "north" and "south." The north basin has an area of 8.1 km^2, of which 33% is less than 10 m deep, and has a maximum depth of 64 m; the south basin has an area of 6.7 km^2, of which 42% is less than 10 m, and a maximum depth of 44 m. The north basin is oligotrophic to mesotrophic but the south basin is slightly more productive and has a larger littoral with more silty and weedy bays. Although the latitude is 54°N, the wet equable

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climate ensures that the lake rarely freezes over and the surface temperature from June to September averages 16°C.

Limnological research on Windermere provides a background to the work on fish (Fogg 1979), but only a few aspects of changes in the biology of Windermere between 1940 and 1985 have received systematic study. Sutcliffe et al. (1982) have shown that winter concentrations of nitrate and phosphate have increased since 1964, particularly in the south basin (probably from, respectively, agricultural and sewage enrichment), and there has been an associated increase in alkalinity. In the last 5 yr, anoxia has been found at the bottom of the south basin's hypolimnion in late summer. Neither the precipitation nor the lake waters of Cumbria show evidence of an increase in acidity over the period 1955–85.

Direct evidence of changes in the abundance of invertebrate food for perch and young pike is more difficult to obtain, but some changes may have occurred (McCormack 1970), notably an increase in *Asellus* in the perch's diet between 1934 and 1963 and the arrival in Windermere of *Crangonyx* in 1960. Crude estimates of the abundance of summer zooplankton show only a possible slight increase since 1970, but do suggest a 10-yr cycle related to temperature (George and Harris 1985). An abundance of the cyprinid the roach (*Rutilus rutilus*) is often regarded as an indicator of lake enrichment. Occasional individuals have been caught in Windermere since 1941 but it has not established itself in any numbers.

Fish of Windermere

Apart from the perch and the pike, the relatively simple fish fauna consists mainly of brown trout (*Salmo trutta*), Arctic charr[2] (*Salvelinus alpinus*), eels (*Anguilla anguilla*), minnows (*Phoxinus phoxinus*), and threespine sticklebacks (*Gasterosteus aculeatus*). The dietary relationships of these species are described in Frost (1946) with additional and later information in Frost (1954), McCormack (1970), Craig (1978), and Kipling (1984b).

Historically there were commercial net fisheries for all the large species since at least the thirteenth century (Kipling 1972), and there still is a small commercial plumb-line fishery for charr. The net fisheries began to be phased out towards the end of the nineteenth century; there had been overfishing of the charr, and sport fishing for salmonids became more important. Tourism developed in the nineteenth century and, with it, angling for perch. This perch angling continued until 1939; since 1945 it has declined, largely because of an increase in other, incompatible, water sports.

Indirect evidence from this angling and some biological data (Allen 1935, 1938) show that between about 1920 and 1939 the littoral fish fauna was dominated by a dense population of small perch and a moderate population of large pike; brown trout were present in smaller numbers, and the charr were pelagic except when spawning. This was the background to Worthington's (1950) project.

Experimental Fishery

After trials, perch were harvested annually between 1941 and 1947 in the north basin and, at a reduced rate, until 1964 in part of the south basin. A total of 90 Mg was sold to be canned for human food. Fish were captured in unbaited wire-netting traps set on the bottom at depths between 2 and 7 m during the spawning season from the end of April until the middle of June. Removal of pike began in 1944–45 and has since continued with much the same effort. Gill nets of 64-mm (bar) mesh are set in shallow water and moved round the lake from October until February until all areas have been fished. Between 1944 and 1948 about 5 Mg of pike was sold as fresh food (Table 1).

Other Information

Tagging experiments (Kipling and Le Cren 1984) and other evidence showed that it is justifiable to consider the perch and pike in the north and south basins as discrete populations.

Other species have not been studied with the same intensity as have the perch and pike, but some quantitative data are available for the charr. Autumn-spawning populations of the charr in the north basin increased between 1945 and 1972, perhaps because of reduced predation from large pike (Kipling 1984a).

Methods

Sampling

Use has been made of shore seines, gill nets of various meshes, and traps of different designs and meshes to obtain samples of perch and pike, but the main analysis of changes in the population dynamics has been based on the catch and effort statistics of the fisheries and, for perch, samples obtained from three (later four) representative groups of traps. After the end of intensive removal of perch (in 1947 in the north basin, part of the south basin in 1951, and the rest in 1964), data from the sample groups of traps were supplemented by five groups of traps where the perch were counted and returned alive. In contrast, the removal of pike by gill nets continued throughout the period, providing both catch statistics and material for examination.

The standard "Windermere" perch trap is unselective for size between 90 and 300 mm but, during the spawning season, is highly selective for spawning fish and for males. Nearly all males mature when nearly 2 yr old, most females when nearly 3, and a proportion when 4. All mature fish are big enough to be retained by the traps (Le Cren et al. 1977), so the recruited stock is essentially the adult stock although a few immature females are caught.

The selection curve for the 64-mm pike gill nets ranges from 550 to 650 mm; fish up to the largest size occurring will be caught (Frost and Kipling 1967). The age at recruitment depends upon growth and sex; some 3-yr-old females are caught and nearly all 4-yr-olds, and most males are not recruited until 5 yr old. The majority of both male and female pike first spawn when nearly 2 yr old (Frost and Kipling 1967), so the gill nets catch only adult fish.

All fish were measured, sexed, and aged (and past growth back-calculated) from the opercular bone (Le Cren 1947; Frost and Kipling 1967), unless the catches were large when stratified subsamples were processed (Le Cren et al. 1977).

Methods of Analysis and Interpretation

For the perch fishery, the unit of effort used was one trap fished for a season (usually 6 wk). The methods used to adjust for year-to-year variations in vulnerability, to explore other sources of error, and to "back-calculate" the situation when the

[2]The spelling differs from that (char) used in *A List of Common and Scientific Names of Fishes from the United States and Canada* (American Fisheries Society) and is preferred by the author.

TABLE 1. Chronology of principal events in Windermere fish population study.

Time period	Fishing	Population	Recruitment	Growth
		Perch		
1921–41	None	Large, approx. 6 million	Moderate, relatively stable	Slow, l_∞ approx. 180 mm
1939–41	Trials			
1941 spring	Start of intensive trapping	High F, fall in numbers		Immediate increase
1947–54	North basin trapping, ended, sampling continued	Low, approx. 1 million, stable	Weak, but varied with temperature	Successive year classes grew faster, temperature correlated
1955 and 1959		Increased to approx. 5 million, biomass > 1941	Very strong south basin (1955), very strong both basins (1959)	
1960–65			Weak	l_∞ approx. 280 mm
1964	South basin trapping ended			
1965–75	Sampling continued	Approx. 1 million, stable, biomass = 1941	Moderate, relatively constant	Rapid
1976		Disease, 98% adult mortality		
1978–85		Increasing, fluctuating high M	Moderate to strong	Rapid
		Pike		
1921–41	None	Moderate, approx. 3000, mostly old	Low, stable	Moderate
1943–44 winter	Trials			
1944–45 winter	Gillnet fishery began	High F, rapid reduction	Increased	
1947–54	Continued	Approx. 1400, <6 yr old		Moderate, temperature correlated
1955–59		Fluctuating, 2000–4400	Varied with temperature	
1960–65				Poor, not temperature correlated
1965–75		Decreasing to 1000	Poor	
1976		Fell to 800	Decreased	Good
1978–85	Continuing	Increased to 1400	Moderate	Good

fishery started in 1941 are described in detail in Le Cren et al. (1977). The analysis was based largely on Paloheimo's (1958) virtual population method.

For the pike fishery the unit of effort was one 27 × 3 m gill net fished for 24 h. Estimates of population and mortality were obtained by combinations of catch curves (CPUE/age), tag recapture data, and virtual population analyses (Kipling and Frost 1970).

In many of the analyses and interpretations for both species, it has proved rewarding to compare the vital statistics for successive year classes or cohorts. So far, interpretations have relied largely on correlation and regression analyses and simple predictive models based upon them.

Results

Numbers and biomass

The perch population in the whole lake was rapidly reduced from just over 6 million in 1941 to about 1 million in 1950 as a result of the intensive fishery which used 700 traps over most of this period. Up to 1951 in the south basin and 1961 in the north basin the population remained low and then increased rapidly to about the 1941 numbers; it then declined again to a relatively steady level of between 1 and 2 million from 1965 until 1976. The biomass showed a similar trend from 136 Mg in 1941 to a low of 45 Mg in 1949. Between 1957 and 1962 the biomass increased to 266 Mg in 1962 and then fell to a relatively stable level of 130–160 Mg (1966–76) (Fig. 1). Three points are immediately clear: (a) in the north basin the population did not start to increase until 14 yr after the end of the intensive removal of perch (in the south basin the increase took place while some removal was still continuing, but occurred at much the same time as in the north basin), (b) in the 10 yr between 1965 and 1975 the population numbers were relatively stable at a much lower level than in 1941, but the biomass was stable at a level similar to that in 1941, i.e. there were fewer but bigger perch, and (c) the extent of the reduction of the stock was greater in the north than the south basin, perhaps because the fishery was more intense on the smaller littoral area.

The population of the pike fell rapidly in the first year of the fishery, but then increased again to fluctuate between a number similar to that in 1941 and one twice as large. The biomass similarly fell, then fluctuated, but always at a level below that of 1941. So, up to 1970, the pike were present in larger numbers of smaller fish. Since 1970, numbers and biomass fell, until by

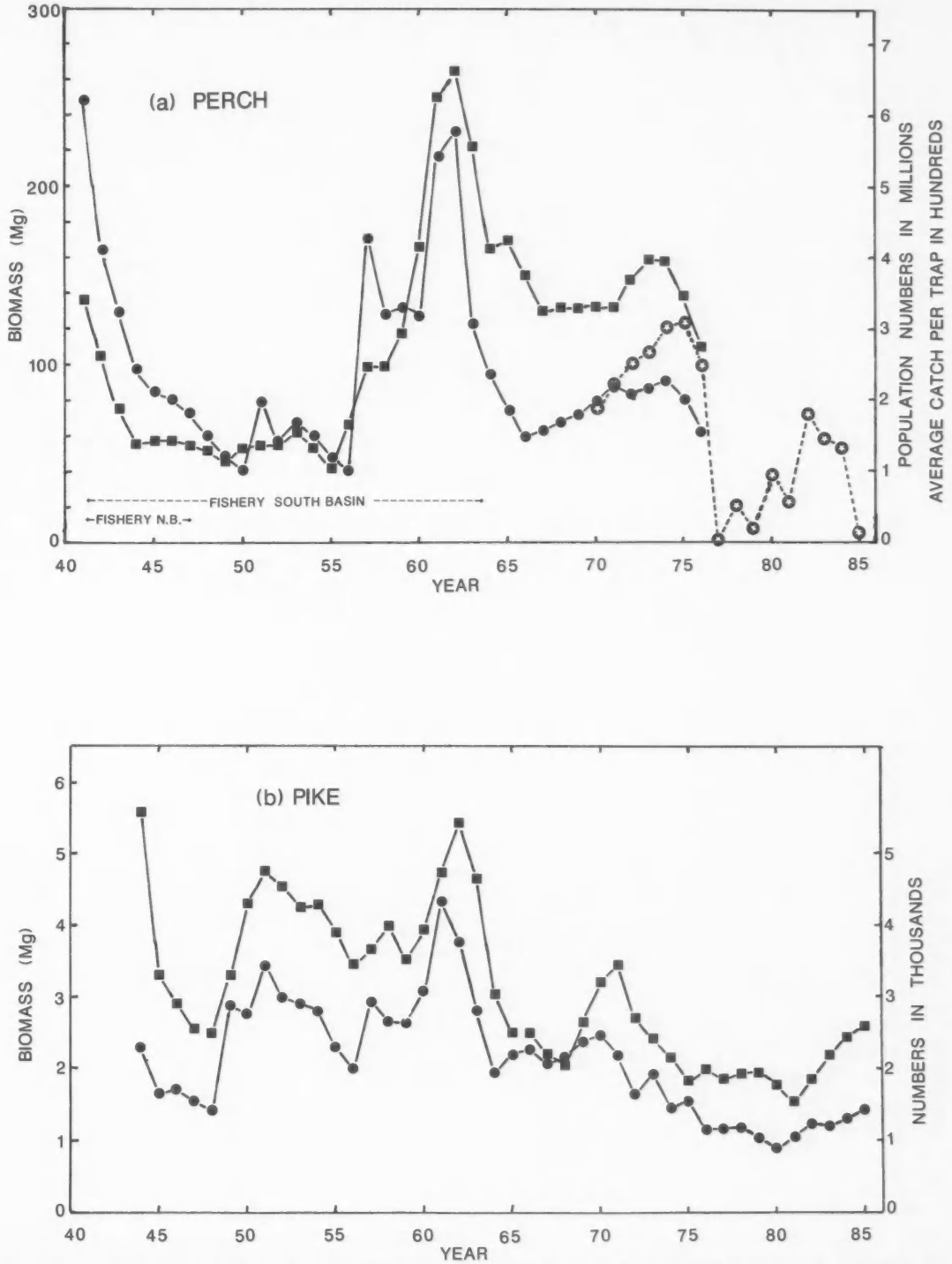

FIG. 1. (a) Estimated numbers (●) and biomass (■) of perch age 2 and older in the whole of Windermere from 1941 to 1975. For the years 1970–85 the average catch per trap (✪) is shown to indicate trends since the disease epidemic of 1976. (b) Estimated numbers (●) and biomass (■) of pike age 2 and older in Windermere from 1944 to 1985. Data from Kipling (1984b) and unpublished sources.

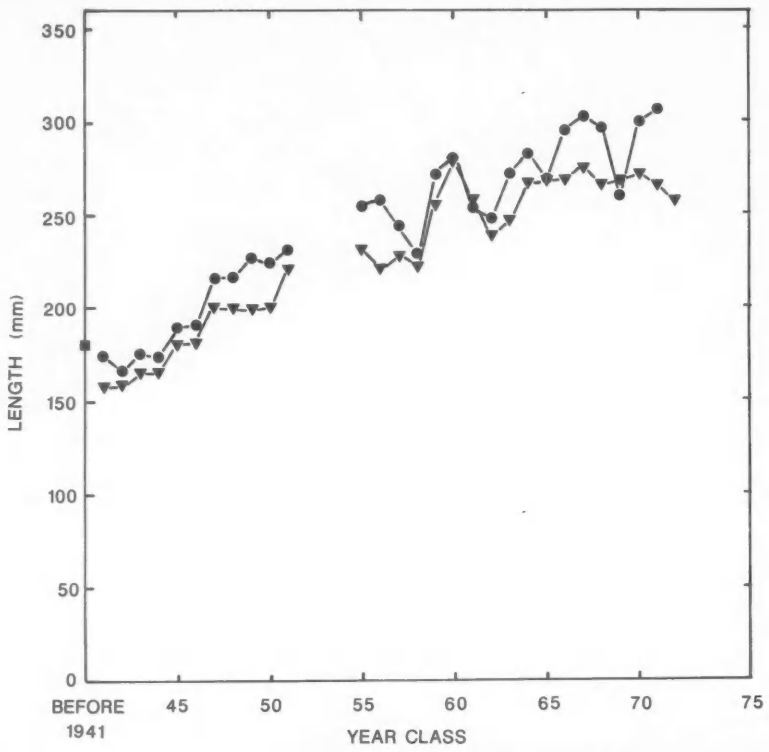

FIG. 2. Growth of successive year classes of perch in the north basin of Windermere. Pre-1941, approximate l_∞ (■); 1941–51 year classes, mean length at 5 yr old; 1955–72 year classes, l_∞; males (▼) and females (●). Data from Le Cren (1958) and Craig (1980).

1980 they were well below those of 1941, but after 1980 they have tended to increase. It must be remembered that the fishery for pike has continued throughout.

Growth

Data for the growth of perch before 1941 (back-calculated from samples taken in 1943 and later years) suggest that a von Bertalanffy model with an l_∞ of about 180 mm fits reasonably well; males grew rather more slowly than females. After the initial reduction in population density in the spring of 1941, there was an immediate increase in adult growth (Fig. 2). Year classes becoming adult in subsequent years up to 1955 did not follow the von Bertalanffy model but had an approximately constant annual increment in weight throughout their adult life. This was highly significantly correlated with summer water temperature, and when adjusted for this, the residuals were highly significantly correlated with population density (from 1941 to 1950 was the period of falling biomass Fig. 1a) (Le Cren 1958 and Fig. 2).

After 1955, perch growth could again be empirically modelled by the von Bertalanffy formula, but an increase in growth continued, albeit at a slower pace, up until the 1964 year class after which there was little trend in l_∞ which averaged 269 mm for males and 288 mm for females (Craig 1980 and Fig. 2). The von Bertalanffy statistic K varied from cohort to cohort and was correlated with l_∞; strong, slower growing year classes such as that of 1959 tended to have a lower K and a higher survival rate. Summer water temperatures continued to have an influence on growth in the later years.

The von Bertalanffy model has provided a good empirical approximation of the growth of pike. The rate of pike growth falls into three periods: the year classes from 1944 until 1959 when growth was moderate and strongly influenced by temperature, from 1960 to 1965 when growth was poor and not related to temperature, and from 1968 to 1978 when growth was good and the relationship with temperature was not statistically significant (Kipling 1983a and Fig. 3).

Production

Total annual production (in the ecological sense) of adult perch between 1961 and 1972 ranged from about 2 to about 15 $g \cdot m^{-2}$ (Craig 1980), while adult pike production between 1944 and 1962 ranged from 0.1 to 0.25 $g \cdot m^{-2}$ (Kipling and Frost 1970). Female perch and pike expend a large proportion of their total production on eggs. Estimates of the production of 0 and 1 group fish are more speculative, but emphasise the relatively large proportion of production that takes place before recruitment (Le Cren 1962). The production of each year class depends largely upon its numbers but also on its growth and survival. The rates of adult production of perch in the 1959–75 period must have been greater than that before 1941 because the biomass (B) was similar but the specific growth rate (G) was

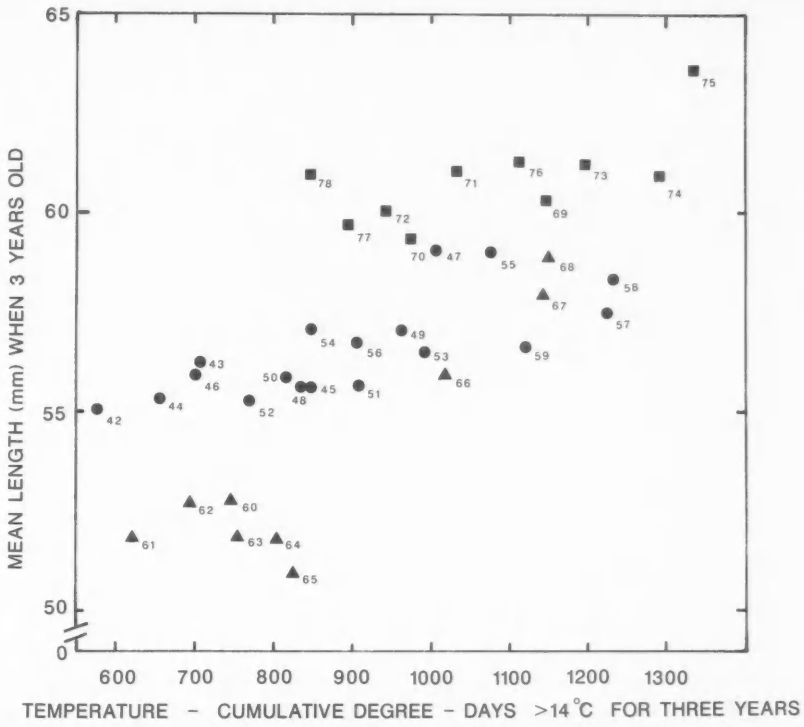

FIG. 3. Growth of pike in Windermere in relation to summer water temperatures. Mean length of females at 3 yr old of year classes from 1942 to 1978 plotted against cumulative degree-days over 14°C during first 3 yr of life. Year classes: ●, 1942–59; ▲, 1960–69; ■, 1969–78. Data from Kipling (1983a).

faster (production = *GB* (Ricker 1975)). Estimates have also been made of the probable consumption of food by the pike (and perch); these show that for certain sizes of pike at certain times, the biomass of available perch of a suitable size might not have met the needs of the pike (Kipling 1984b).

Recruitment

Some changes in fecundity in relation to size (i.e. relative fecundity) have occurred in pike and probably perch (Craig and Kipling 1983; Kipling and Frost 1969), but there has been no correlation between population fecundity and the strength of the resultant year class on recruitment. Parental stock biomass is therefore a reasonably good measure of the number of eggs laid, and plots of year class strength against parental stock biomass (Craig and Kipling 1983 and Fig. 4) do not show an obviously simple stock–recruitment relationship, although Craig and Kipling (1983) calculated curves and showed that plots of ln (R/P) on P were significant for both perch and pike. The plots for the two species differ (Fig. 4a and 4b); whereas in the perch, low parental stock numbers did give rise to both low and very high recruitment, in the pike there is no year in which a small parent stock gave rise to a strong year class. No strong year class of perch arose in a year when adults were abundant, but a similar effect is not so apparent in the pike (although the highest stock biomasses gave rise to only moderate year classes). Survival from the egg to an age of 2 has varied 300-fold in the perch and sevenfold in the pike.

For both species there is a strong correlation between survival of the young and summer water temperature in the year of hatch (Craig and Kipling 1983 and Fig. 5). For perch between 1961 and 1975, $r^2 = 0.73$, i.e. 73% of the variation in year class strength could be accounted for by temperature. For pike between 1944 and 1980, $r^2 = 0.37$, but for 1944–62, $r^2 = 0.78$ (Kipling and Frost 1970). Water temperature in July, August, and September of the year of hatch was thus a major factor influencing recruitment in both species; for the pike, there is evidence that autumn temperatures also had an effect (Kipling and Frost 1970; Kipling 1984b).

Between 1959 and 1974 there was also a negative correlation between the logarithm of perch year class strength and the biomass of adult perch in the year of hatch (Craig 1982); this could explain the descending right-hand limb of the stock–recruitment relationship in Fig. 4a and the fact that large spawning stocks have never given rise to strong year classes. There is also a correlation between the number of young pike and the mortality of young perch. Craig (1982) and Craig and Kipling (1983) have combined these correlations into a simple model:

$$\ln R = C_0 + C_1T + C_2P + C_3 \ln Y$$

where R = number of perch recruits, T = temperature in the year of hatch (measured as "degree-days" over 14°C), P = biomass of adult stock (megagrams) in the year of hatch, Y is pike cohort strength in the same year, and C_0, C_1, C_2, and C_3

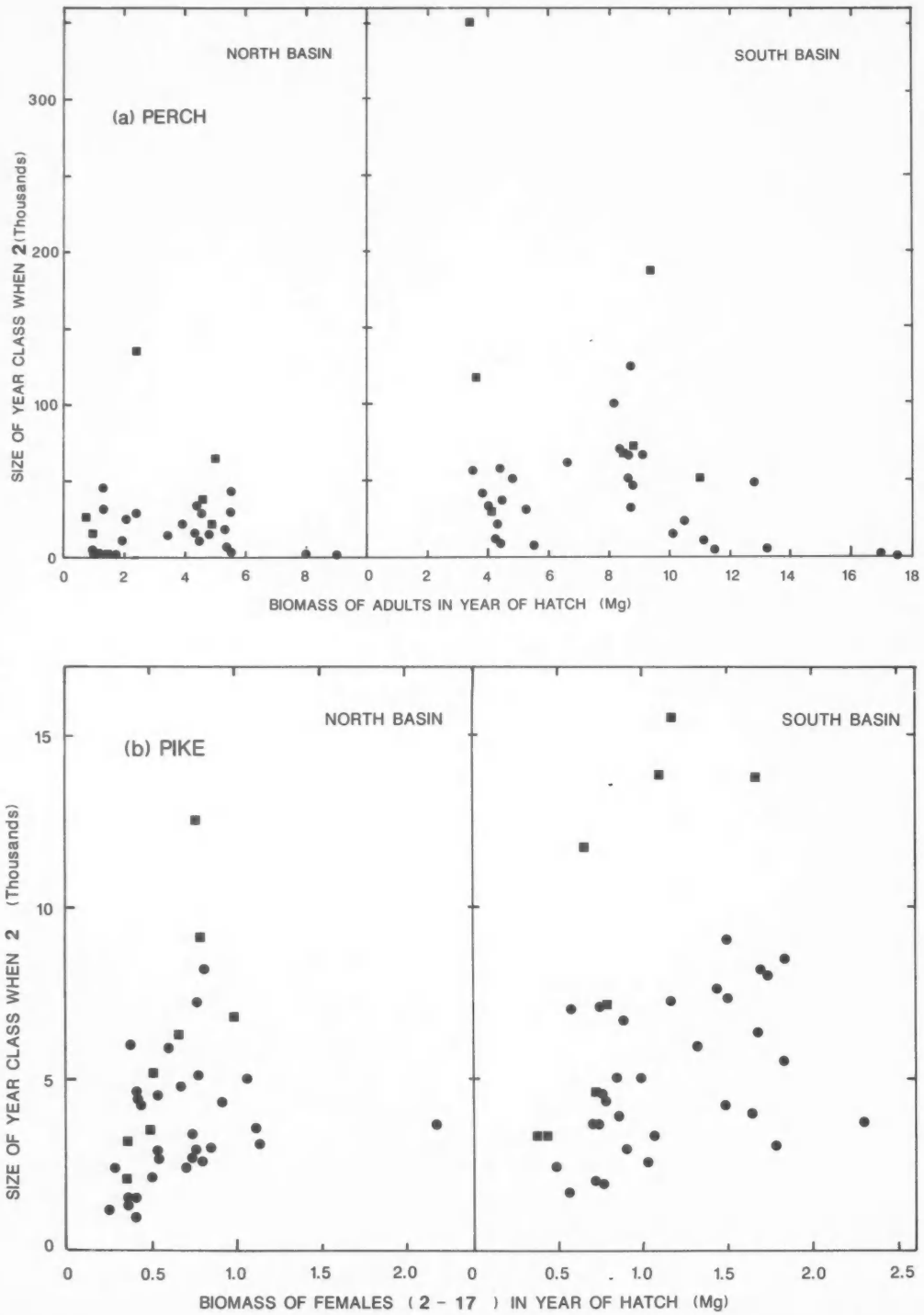

FIG. 4. Stock–recruitment data from the north and south basins of Windermere. ■-year classes hatched in the seven or eight warmest years. (a) 1941–75 perch year class strength plotted against total adult biomass in year of hatch; data from Craig et al. (1979). (b) 1944–82 pike year class strength plotted against female adult biomass in year of hatch; data from Kipling (1983b).

are constants, C_2 and C_3 being negative. For the years from 1959 to 1974, $r^2 = 0.87$ for the north basin and 0.91 for the south basin and both were highly significant. This means that over that period the model could account for about 90% of the variation in perch year class strength. The partial correlation coefficients were also significant. Approximately 75% of the variation could be accounted for by temperature alone, 85% by temperature and adult perch biomass, and 90% by the model incorporating pike year class strength as well.

Kipling and Frost (1970) and Kipling (1984b) have postulated that growth in the first year is critical in determining pike survival and hence year class strength; the young pike have to achieve a length of 200–250 mm before their first winter to avoid predation by pike 1 yr or older. Temperature probably acts largely through growth, influencing both the rate of growth and the length of the growing season into the autumn. There is a positive correlation between the strength of the pike year class and that of the perch in the same year; this might be expected if both are correlated with temperature. However, the availability of perch of the right size as food may also be important (Kipling 1984b).

Adult Mortality Rates

Although the natural mortality rate (M) of the adult perch before the start of the fishery in 1941 could be estimated only indirectly, it was probably about 0.42 (Le Cren et al. 1977); the rate for males was slightly higher than that for females. During the years of the trap fishery, fishing mortality rates (F) were imposed of 1.21 in the north basin and 0.31–0.45 in the south basin, giving total mortality rates (Z) between 0.73 and 1.71.

After the end of the period of intensive removal of perch, M appeared to be relatively constant at a rate similar to that before 1949, i.e. $M = 0.41$ in the north basin and $0.41 - 0.50$ in the south basin. In 1969 the rates increased and until 1975 ranged from 0.65 to 1.28. The mortality rate appeared to be remarkably constant for mature perch within each year class (although somewhat greater for males than females) but has varied between year classes (Craig et al. 1979). Craig (1980, 1982) has shown that the year classes between 1959 and 1972 showed a highly significant positive correlation between M and the K statistic in the von Bertalanffy growth formula; faster growing cohorts survived less well (although the reverse is the case for prerecruitment survival and growth (Craig 1982). (Craig (1985) reviewed the correlation between growth and survival in fish as a fundamental biological phenomenon.)

Before the start of the gillnet fishery in 1944, adult pike had a mortality rate (Z) of between 0.40 and 0.50; males had a slightly higher rate than females and pike in the south basin a higher rate than those in the north basin. Nearly all this mortality can be considered natural (M), but a little will have been caused by angling and one commercial fisherman.

Initially, the gillnet fishery generated an F of 1.35–1.90, but after the first 2 yr, F fell so that the total mortality (Z) was between 0.75 and 0.93, about half of it due to the fishery. There was no evidence that the natural mortality rate changed significantly; Craig and Kipling (1983) give values of $M = 0.30$ and $F = 0.65$ as general averages for the whole period from 1944 to 1980.

Events since 1976

In 1976 an epidemic disease of perch, which had been spreading through Britain, reached Windermere and caused mortalities up to 98%, especially among adult fish (Bucke et al. 1979). The primary infective agent has not been identified but the fish probably die from secondary infections entering through skin lesions. Since 1976 the disease has become less virulent; in 1986, fish bearing lesions symptomatic of the disease were still caught but the proportion of these diseased fish had fallen. Because a full analysis of population changes requires samples for age analysis for at least 3 yr after recruitment, it is not yet possible to produce quantitative data for recent years comparable with those available before 1976. However, simple catches-per-unit-effort for the years 1966–85 are shown in Fig. 1. After the dramatic fall from 1976 to 1977, catches have fluctuated but tended to increase to levels approaching those of 1966–70. The catches of young perch suggest that recruitment since that of the 1975 year class has continued at rates similar to those in the early 1970s in spite of the apparently very low abundance of the adult spawning stock. No fish more than 5 yr old has been caught since 1976, and the mortality rate of adults must have increased to more than 1.1.

Before 1976, only a small proportion of perch caught in traps in spring were not mature spawning fish, but since 1977, immature fish were often more abundant than mature fish among the trapped females. This may be partly due to larger numbers of immature perch entering the traps and partly to there being a higher proportion of immatures among the older fish; perhaps mature fish are more susceptible to the disease? In contrast, for the first time in Windermere, a few females have been found mature when just 2 yr old. The growth of the perch has continued to be rapid, although the high mortality rate means that the average size remains relatively small.

The population of pike was relatively low from 1972 onwards (Fig. 1b), recruitment has been relatively poor, but growth has been good (Fig. 3). There was evidence that the pike tended to move out of the shallows in 1976, perhaps to feed on charr (Kipling 1984b). Since 1981 the numbers and biomass of pike have tended to increase again.

Discussion

Introduction

Any general model attempting to explain the observed changes in the perch and pike populations in Windermere over the period 1940–85 will need to take account of the following principal features and events:

(1) The state of the unperturbed populations before 1941. These consisted of a dense population of slow-growing perch and a moderate population of fairly fast-growing pike which fed mainly on these perch. This situation appeared to be typical of most other similar lakes in the area, and many elsewhere. An exception was Ullswater, a lake similar limnologically to Windermere except that it contained perch but no pike. Here the perch biomass density was about 20% of that in Windermere and the average individual adult size about twice that in Windermere (McCormack 1965). The paradox that in most lakes the pike did not control the density of the perch at a lower level needs to be explained.

(2) A rapid initial fall in numbers and biomass with the advent of the fisheries. The pike quickly recovered its numbers, but the perch, at least in the north basin, remained at a low density for several years after intensive removal ended. The perch showed some large fluctuations in numbers, but appeared to become relatively stable during the decade beginning in 1965; they then

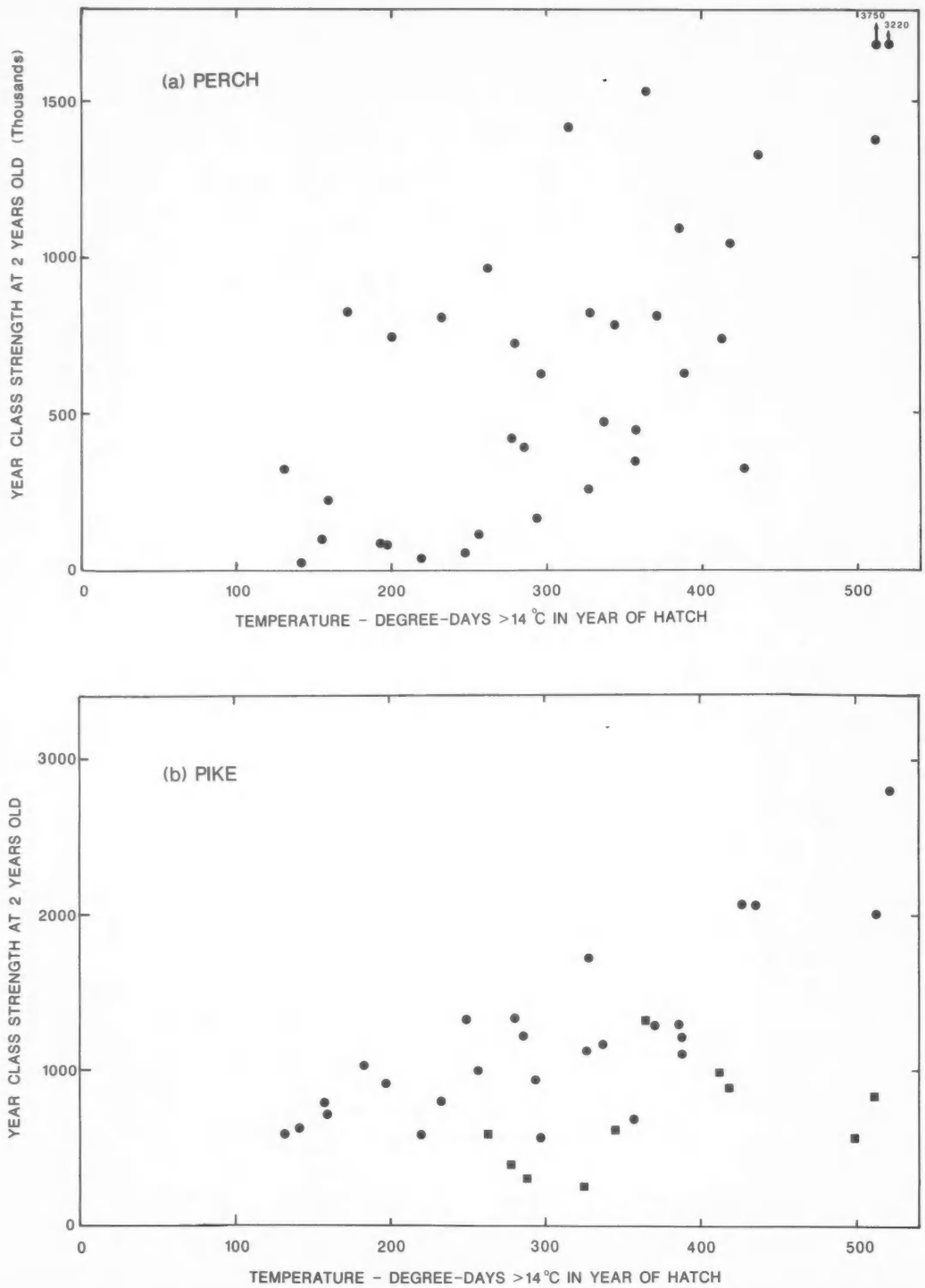

FIG. 5. Year class strength plotted against summer water temperatures (degree-days above 14°C) in year of hatch. (a) Perch, 1941–75; data from Craig et al. (1979); (b) pike, 1944–78; data from Kipling (1983b).

had a biomass similar to that before 1941, but a population structure quite different, consisting of fewer, faster growing, fish. Pike have been relatively more stable, but have shown some significant fluctuations.

(3) The growth rate (and, less importantly, the fecundity) of both species has changed. That of the perch increased greatly and that of the pike fluctuated.

The factors that have so far been identified to explain the above features are (a) the abiotic effects of summer water temperatures on both growth and recruitment, (b) the effects of population density on growth (and, less importantly, on specific fecundity), (c) intraspecific and interspecific predation, both probably strongly size selective and the mortality they generate depending upon the relative abundance of predator and prey, (d) a positive correlation between adult mortality rate and adult growth rate (this certainly occurs in the perch and is probably a basic phenomenon in all fish), and (e) interactions between the above four factors. These factors will now be discussed in more detail with examples of how they may have operated.

Temperature

One of the most striking findings of the Windermere study has been the effect of summer water temperatures on growth and recruitment of both perch and pike (Fig. 3 and 5). Recruitment of the perch varied up to 300-fold and that of pike sevenfold. Up to 75% of this variation in both species could be accounted for by temperature.

It is very probable (both from these observations and unpublished experiments) that the optimum temperature for perch growth when food is abundant is higher than that normally experienced in Windermere. Temperature may also act on the survival of the young through growth; e.g. rapid growth out of a size vulnerable to predation and, in pike, the achievement of a critical size before the first winter will both enhance survival. The timing of events in the food web so that suitable food is available at critical periods in development may also be important; both Smyly (1952) and Craig (1978) have observed what may be a shortage of food for perch fry in July. A much more detailed study is needed before we can understand how temperature acts on early survival.

Windermere is not unique in showing correlations between growth and temperature and recruitment and temperature; some synchrony in year class strength was shown in lakes in the area (Le Cren 1955; McCormack 1965). Perch lakes in the northwest of Britain may provide examples of the increasingly important influence of abiotic factors towards the limits of the ecological range of species (Watt 1962); perch are found further north but perhaps only in more continental climates or shallower lakes where summer water temperatures are higher than those in Windermere.

Mean summer water temperatures and their variance have been similar in each decade over the period, but the pattern of annual fluctuations has varied; a succession of three or four cool or warm summers can have an effect on the fish populations different from that of alternating hot and cold ones.

Density-Dependent Growth and Fecundity

The perch responded to the initial reduction in population by an increase in growth rate. Adult growth (when adjusted for temperature fluctuations) was closely related to population density from 1941 to 1955 and this continued into the 1965–75 period when a population about one sixth of its original level consisted of fish of an average weight six to seven times what it had originally been. The changes in pike biomass have been much smaller (largely because of responses in population numbers), and there is little evidence of any density-dependent response in growth.

There has been a fecundity response in both species. In perch, the specific fecundity (or "relative fecundity," i.e. eggs per gram of fish weight) appeared to be the same in 1944 and 1960 but had increased 46% by 1980. Absolute fecundity has increased greatly with the increase in the size of the fish. Pike showed a negative correlation between fecundity and parental stock biomass 2 yr earlier; the average size of female spawning pike has not varied as much as has that of the perch. The density dependence of fecundity has, however, been small relative to the changes in population and fluctuations in recruitment; in neither species was there any correlation between population fecundity and the size of the resultant year class on recruitment.

There was some immediate increase in perch growth in the summer of 1941 after the first season's fishing, but after that, the increases were shown by each successive year class, which appeared to respond to the density in its early adult (i.e. third and fourth) years. There was also a delay in the response in fecundity, and pike fecundity appears to be influenced by density 2 yr previously. (The natural mortality rate of perch also seems to be relatively constant throughout adult life and thus "fixed" in the first year or two of maturity (Craig et al. 1979; Craig 1982).)

Intraspecific and Interspecific Predation

Perch feed on zooplankton, benthos, and fish and are frequently cannibals. The four studies of perch diet in Windermere (Allen 1935; Smyly 1952; McCormack 1970; Craig 1978) differ in the emphasis that they give to various features in the diet, but all tend to show that although perch fry may be eaten by all sizes of perch (including larger fry of the same brood (Smyly 1952)), perch do not normally become piscivorous and thus cannibals until they are over about 180 mm in length. Le Cren (1958) estimated that before 1941 only 3–6% of the biomass of perch would have been feeding on perch. In spite of the decrease in total biomass, that portion large enough to be cannibals would have increased through growth by about 1950. In subsequent years the much greater size of most of the adult perch would have meant that nearly all the adult biomass will have been potential cannibals. The size of food items actually eaten by perch will depend upon the density and availability of particular prey items as well as their size; large perch will eat zooplankton when it is abundant. Nevertheless, as Allen (1935) and many subsequent authors have pointed out, it will be advantageous for a fish to eat the larger items among those readily available. For perch above about 180 mm in late summer, young perch are likely to be among these preferred prey items. Although young pike will also be eating young perch, in most years the biomass of perch feeding on perch is likely to have been larger that that of pike feeding on perch. Craig and Kipling's (1983) model of perch recruitment has demonstrated the importance of the abundance of older perch as a negative factor in year class success, and it is very likely that this factor operates through cannibalism.

Cannabilism, and thus population control by a density-dependent factor, may be an explanation for the sparser population of perch in Ullswater where the average adult size was large enough for many of the adults to feed on their own young. In

Windermere before 1941, the biomass of perch large enough to be piscivorous may have been too small to exercise this control.

The pike, after the first few weeks of life, is almost entirely piscivorous. It is also selective in the size of its prey which, although it can range to up to 45% of the length of the pike, tends to be about 20% when perch is the prey (Frost 1954). Young-of-the-year pike feed on perch of the same age, and Craig and Kipling's (1983) model of perch recruitment shows that this can have a significant effect on perch year class strength. The stock of older pike before 1944 must have fed most heavily on the perch >140 mm, i.e. the larger and older adults. Estimates of the rate of consumption of food by the adult pike (Kipling and Frost 1970) show that after an initial decrease in 1945–48, food consumption from 1949 to 1953 was greater than it had been before 1944. This was the time when the perch population was at its lowest level; the failure of the perch to recover its abundance after the cessation of the fishery in the north basin may have been due, at least in part, to pike predation.

Among the fish eaten by pike are other pike. Because pike are relatively less abundant than other species such as the perch, they occur infrequently in the stomachs (Frost 1954), but cannibalism may be a significant part of the relatively low rate of natural mortality among all but the largest pike. Kipling and Frost (1970) have postulated that predation by pike 1 yr older may cause heavy mortality among 0 group pike that fail to reach a length of about 200 mm by the end of their first summer; this may be the mechanism by which temperature operates on year class strength. Density-dependent cannibalism within the 0 group fish may also be important but difficult to measure under field conditions. Kipling (1983b, 1984b) has emphasised the probable importance of the abundance and growth rate of 0 group perch as food for 0 group pike. This could explain the weakness of pike year classes in the late 1960s when young perch were abundant but possibly growing too fast to be of a size suitable for young pike to eat. Pike fry have also been found in the stomachs of larger perch, but the quantitative significance of this cannot be estimated.

Thus, the predator-prey relationship between the pike and perch is not just the simple one of pike eating perch. The tendency for both species to require food of roughly an optimum size in relation to their own size and below a maximum size (45% of its own length for a pike) means that only some of the potential prey are available. Larger perch can compete with pike for small perch as prey and will normally be much more numerous than the pike. Perch over 180–200 mm may be important predators on their own young and even prey on young pike, but larger pike are likely to be the major predators on pike.

Relationship between Growth Rate and Mortality Rate

Craig (1980, 1982) has shown that for adult perch belonging to the year classes from 1959 until 1972 there was a strong correlation between mortality (Z) and growth (measured by K in the von Bertalanffy formula). The 1955–58 year classes did not show the same relationship; nor was it shown among juvenile fish. A similar correlation has been shown by Beverton and Holt (1959) for other species. The 1964–72 year classes grew very fast and were weak in abundance compared with the 1955 and 1959 year classes that had been dominating the population. If this growth rate related mortality has a physiological cause, it can represent only part of the total natural mortality and may become apparent only when growth is very fast and other causes of mortality relatively low. Nevertheless, it is a factor that should be taken into account; physiological ageing may contribute to natural mortality even when predation or other causes seem to be the major ones.

Interactions

Craig and Kipling's (1983) model of perch recruitment includes three factors: temperature, adult perch biomass, and number of young pike. Normally, temperature is the dominant factor (and it may operate first in time), but the data from different periods show that temperature was not always the major factor affecting growth or juvenile survival. The failure of the 1947 year class of perch might have been caused by a quite exceptionally cold and late spring when Windermere was frozen up to a few days before the normal start of the spawning season (Kipling 1976). The weakness of the 1949 and 1955 year classes of perch in the north basin relative to what might have been expected from their hot summers (and the success of the 1955 year class in the south basin) might have been a result of a rate of food consumption by the pike large relative to the population of perch available (Craig 1982) and, perhaps, the presence by 1955 of some faster growing older perch big enough to be cannibals. Kipling (1983a) has attributed the poor growth of the pike and lack of any correlation with temperature between 1960 and 1965 to a shortage of perch of the right size available as food.

There is evidence from both perch and pike that temperature influenced both growth and recruitment in both species before 1941, but its effect was less marked because the populations of both species consisted of a large number of relatively slow-growing year classes. Annual fluctuations in recruitment and growth would thus have little effect on the whole population. The increased mortality caused by the fisheries reduced the age range, increased perch growth, and thus led to variations in recruitment and growth having a much greater effect on the total population. A similar effect became apparent with the fast-growing and short-lived perch year classes of the 1964–72 period.

Nearly all the variation in perch recruitment can be accounted for by temperature and predation by pike and older perch (at least for the period from 1958 to 1971), so it does not seem necessary to invoke any other factors. Nevertheless, some intrabrood density-dependent effects on growth and survival might be expected, and it is possible that they may occur, or be one of the mechanisms through which temperature operates. Such density-dependent effects may have been more important within young perch before 1941, and their absence at low population levels may have been one of the causes of the high prerecruitment survivals apparent after 1976.

Summary of Changes over Each Period

The various factors and interactions that have been discussed above can be applied to each of the periods listed in Table 1.

Before 1941 both the perch and pike were relatively long lived, with an only moderate rate of mortality. Much of this perch mortality, especially that of the larger perch, would have been caused by pike predation. Some of the mortality among all but the largest pike was due to cannibalism. The perch population was dense; there was little control of recruitment by cannibalism because few of the perch grew big enough to be piscivorous. The pike population was controlled at a moderate level by cannibalism. The growth of the perch was slow because of the dense population. The effect of temperature on growth

and recruitment was present but damped by the extended age structure of both populations.

In the early years of fishing (1941–45 for perch and 1944–47 for pike) there was the rapid decline in numbers and change to a younger age structure typical of the imposition of an intensive fishery on an unperturbed stock. The pike responded rapidly to this by an increase in recruitment due to a lowering of density-dependent cannibalism; this led to an increase in the population of young pike. The reduction in the perch population led to an increase in growth rate, but the momentum of this took a few years to develop; there was initially not much change in perch recruitment. After the end of the perch fishery in the north basin (1948), the perch population did not increase because of weak recruitment caused by predation, even in the hot year of 1955 where the brood was strong in the south basin. This suggests that a pike population large relative to the perch population, coupled with the growth of older (unfished) perch, suppressed survival of the 1955 year class in the north basin. The 1959 year class was exceptionally strong in both basins, and this brought the total population back to a biomass greater than that in 1941. (These events emphasise the importance of variations in abiotic factors acting on populations that have become less stable because of a younger age structure.)

The pike had also responded to variations in temperature, but its numbers had tended to fluctuate round an average rather larger than those of before 1944; 1959 was an exceptional year class for it as well. As the 1955 and 1959 perch year classes grew older and declined in numbers, the perch entered a relatively stable period with a biomass similar to that of 1941 but made up of fast-growing and therefore short-lived year classes. Because of their fast growth, they provided a poor food supply for young pike, and the latter species suffered a succession of weak year classes which led to a decline in numbers.

The period after 1976 has been dominated by the perch disease; this has demonstrated that perch recruitment can be adequate even when spawning populations are very low indeed; this is added evidence of the importance of predation by older perch (very scarce since 1976) and possibly other density-dependent factors. The pike appear to have been able to adapt to a shortage of their principal food, perhaps by turning partly to other species.

Concluding Comments

This 45-yr study of perch and pike in Windermere leads to some general ideas that may be applicable to other fish populations:

(1) Piscivorous species such as the pike that control their own populations by cannibalism will respond rapidly to fishing and other factors by changing their rate of recruitment.

(2) A less intensively piscivorous fish like the perch may still control its own population by cannibalism, but only if it can grow large enough. Density-induced slow growth and selective predation by a large piscivore may lead to a dense slow-growing population. In any consideration of intraspecific and interspecific predation, prey size selection must be taken into account.

(3) Abiotic factors such as temperature may be important, especially towards the edge of a species' ecological range or where fishing has reduced the age range of a population and thus made it more susceptible to environmental fluctuations. Fast-growing populations may have a high growth-related mortality and thus a short age range; they, too, may be less stable, even if more efficient producers.

(4) Rates of growth and natural mortality may change only with successive year classes, each of which may "fix" its growth and mortality at a particular age. This means that changes in whole populations may take some while to develop fully and to become apparent to the observer. It also emphasises the value of the classical cohort approach to population analyses.

(5) Each period in our studies of fish in Windermere has produced new events, interpretations, and ideas which have caused us to modify previous conclusions. Long-term studies have a special value in fishery research.

Acknowledgements

A long-term study such as this one inevitably involves many people; not only those who become authors of published papers but also those who have lifted traps and nets in all weathers or read operculars for age or carried out calculations in the laboratory. In the Windermere fish population study there has been an unusual degree of warm cooperation, and in writing this review and commentary I am grateful to all those colleagues who have contributed to the various aspects of the whole project; I have drawn heavily and freely upon the results of their work. I am also indebted to those who have commented upon drafts of this paper, particularly Dr. John Craig, Miss Charlotte Kipling, and two anonymous referees. Most of the costs of the whole project were met by grants-in-aid to the Freshwater Biological Association from the Development Commission up to 1965 and the Natural Environment Research Council since then. While preparing this paper I have had the support of a Nuffield Emeritus Fellowship.

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Optimal Use of Creel Survey Data in Assessing Population Behaviour: Lake Opeongo Lake Trout (*Salvelinus namaycush*) and Smallmouth Bass (*Micropterus dolomieui*), 1936–83[1]

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Shuter, B. J., J. E. Matuszek, and H. A. Regier. 1987. Optimal use of creel survey data in assessing population behaviour: Lake Opeongo lake trout (*Salvelinus namaycush*) and smallmouth bass (*Micropterus dolomieui*), 1936–83. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 229–238.

Creel survey and independent assessment data on the lake trout (*Salvelinus namaycush*) and smallmouth bass (*Micropterus dolomieui*) populations of Lake Opeongo were evaluated. Annual estimates of total mortality, fishing mortality, and abundance were generated for each population over the period 1936–83. Large variations in survey efficiency, angler efficiency, fishing mortality, and abundance were identified over this period. We argue that a creel survey, which is expected to provide reliable information on fish population dynamics, requires an overall study design which includes collection of data on the number and relative efficiency of different kinds of anglers and periodic assessment studies aimed at providing independent checks on both survey effectiveness and population behaviour.

Les auteurs évaluent des données recuillies au cours d'enquêtes sur la pêche sportive et d'évaluations indépendantes visant des populations de touladi (*Salvelinus namaycush*) et d'achigan à petite bouche (*Micropterus dolomieui*) du lac Opeongo. Ils ont ainsi obtenu des estimations annuelles de la mortalité totale, de la mortalité par pêche et de l'abondance de chaque population pour la période 1936–1983. De fortes variations de l'efficacité des relevés, du succès du pêcheur, de la mortalité par pêche et de l'abondance ont été notées pour cette période. Selon les auteurs, une enquête sur la pêche sportive ne peut fournir des données fiables sur la dynamique d'une population de poisson que si elle comprend la collecte de données sur le nombre et le succès relatif des différents types de pêcheurs et des évaluations périodiques pour obtenir des vérifications indépendantes de l'efficacité du relevé et du comportement de la population.

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The annual survey of lake trout (*Salvelinus namaycush*) and smallmouth bass (*Micropterus dolomieui*) angling fisheries on Lake Opeongo began in 1936 and has operated continuously since that date. Data from this survey have been used by a variety of authors (Fry 1949; Martin and Fry 1973; Emery 1975) to investigate the biology of lake trout and smallmouth bass. These data have also been used as aids in developing and evaluating new analytical techniques for investigating the dynamics of fish populations (Fry 1949; Beverton and Holt 1957; Paloheimo 1958, 1980). The Lake Opeongo creel survey stands as one of the longest and most complete sources of information on the dynamics of freshwater fish populations in the world. An anecdotal history of both the survey methods and the fishery itself has recently been published (McMurtry and Shuter 1985). In this paper, we present a quantitative evaluation of the data from both the lake trout and smallmouth bass populations for the period 1936–83.

The basic set of data collected annually by the survey is summarized in Table 1. Mark–recapture experiments were carried out in the following years: lake trout — 1950–53, 1960–63, 1976–83; smallmouth bass — 1955–56, 1959–60, 1972–73, 1980–81. Catch-at-age and effort data from the creel survey on both populations are summarized in Table 2. These summaries were derived from a complete retabulation of the original catch records. In addition, the figures for lake trout are based on new ages obtained by having a single, experienced scale reader reage the entire lake trout scale collection. We believe this to be the most accurate summary of the Lake Opeongo data published to date.

The basic trends in effort, catch, and catch-per-unit-effort present a broadly similar picture for both populations (Fig. 1) — a picture of increasing effort, increasing catch (particularly after

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TABLE 1. Basic data set for Lake Opeongo creel survey. All information listed was generally taken from each party interviewed and from each fish examined. Over the period 1936–83, the number of lake trout examined annually averaged at 72% of the number recorded as kept by the survey. The comparable figure for smallmouth bass was 48%. Age distributions from examined fish were used to derive the kept-at-age figures listed in Table 2.

Data on fishing parties	Data on individual fish
Date of interview	Date examined
No. of men	Length
No. of boats	Weight
No. of hours fished	Age (from scales)
Location fished	Sex
Angling method (several categories)	Sexual maturity (several categories)
	Stomach contents, no. of items by food type (several categories)
No. of fish caught	
No. of fish kept	Length and weight of each food item (when measurable)
No. of fish examined	

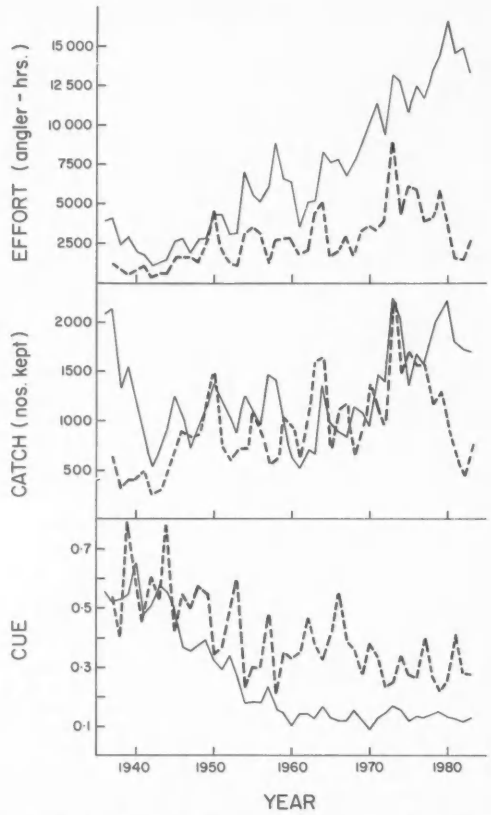

FIG. 1. Variations in the effort, catch, and catch-per-unit-effort (CUE) for lake trout (solid line) and smallmouth bass (broken line) over the period 1936–83. For each species, effort is the total number of angler-hours directed against the species by parties who were interviewed in the survey, catch is the total number of fish that were kept by interviewed anglers, and CUE is the total number kept divided by the total effort.

1965), and declining catch-per-unit-effort. These trends are typical of many developing fisheries and, simply interpreted, suggest that both populations declined significantly in abundance under the increasing fishing pressure of the 1940s and 1950s, but have since stabilized and held their own against the even higher pressures of the 1960s and 1970s. However, this interpretation hinges on two critical assumptions: (a) the catch and effort figures recorded by the survey are consistent indicators of annual total catch and annual fishing mortality rate, respectively; (b) the catch-per-unit-effort figures are consistent indicators of population abundance. There have been a variety of changes in both the survey and the fishery over the years which call both of these assumptions into serious question. These changes are described in detail in McMurtry and Shuter (1985); they are briefly summarized below and in Fig. 2.

Access to Lake Opeongo is restricted to a single point at the bottom of the south arm (Fig. 3). The creel survey operates by interviewing anglers returning to this point. In the early years, the fishery was largely composed of ardent fishermen, assisted by local guides. Both guides and anglers were based at a lodge located at the access point. Most fishing parties would spend part of a day on the lake and then return to the lodge in the evening. Creel survey workers were stationed near the lodge throughout the fishing season and, therefore, were able to interview the great majority of parties on their return. Rapport between the survey workers and the lodge operator was good: if parties returned when the survey station was unmanned, the operator would inform the survey staff and the party would be interviewed. For these reasons, it was felt that survey coverage of the fishery was essentially complete: Martin and Fry (1973) estimated that, for this period, the annual lake trout catch recorded by the survey represented no less than 80% of the total catch taken by the fishery. In the 1950s, a number of changes began which altered the effectiveness of both the survey and the anglers: (a) large numbers of relatively unskilled anglers began to frequent the lake; many of these anglers would stay several nights at campsites around the lake and then leave via the access point at any time during the day; (b) the percentage of guided parties declined, particularly after the closure of the fishing lodge in 1960; (c) in the 1960s, the creel survey station was frequently unmanned during weekdays; thus, many parties leaving the lake on weekdays were not interviewed. The overall effect of these varied changes was to decrease the effectiveness of the survey (in the sense that the percentage of the total catch actually recorded by the survey declined) and to decrease the impact on the population of an average unit of fishing effort, since the average level of skill in the fishery declined.

Given changes of this sort, it is possible that the true historical behaviour of both populations may differ from the rather simple pattern evident in Fig. 1. In the following sections, we show that this is, in fact, the case: catch and effort data alone provide a grossly misleading picture of the historical behaviour of both populations. We also demonstrate that a reliable picture can be developed only by utilizing extensive information, on the populations and their fisheries, derived from both the creel survey and from independent assessment studies.

Statistical Methods and Results

Our reconstruction of the behaviour of both the lake trout and smallmouth bass populations proceeded in several stages. First,

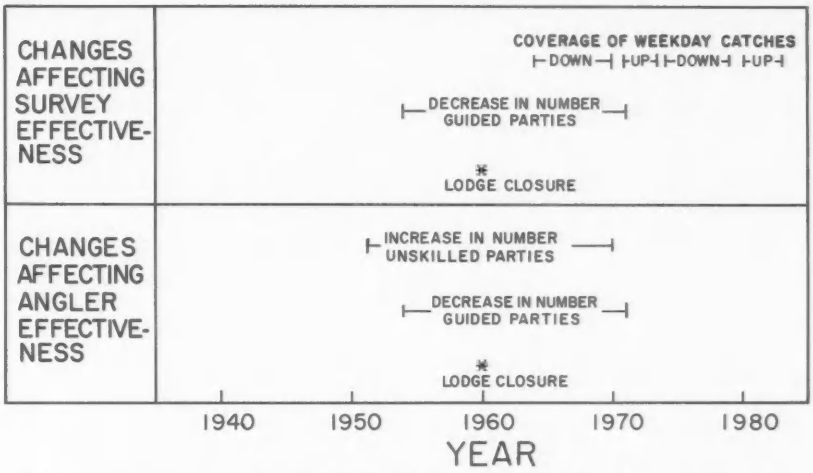

FIG. 2. Summary of changes, in both survey procedures and the fishery itself, which altered both the effectiveness of the survey (i.e. the percentage of parties interviewed) and the effectiveness of the average angler (i.e. the impact on the population of 1 unit of angling effort).

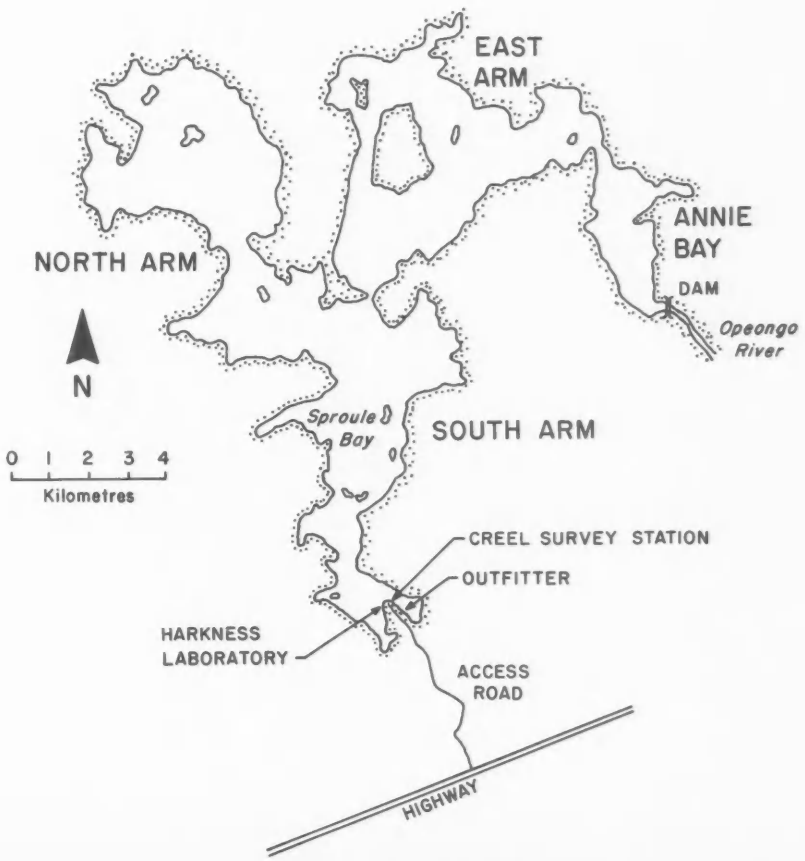

FIG. 3. Map of Lake Opeongo.

TABLE 2. For both the lake trout (not italicized) and smallmouth bass (italicized) populations, annual values for number of fish in each age group kept by anglers, total number of fish kept, and total effort (angler-hours) directed against the population by anglers who caught and kept at least one member of the population (EFK1). These figures are the values recorded by the creel survey and have not been corrected for variations in survey effectiveness.

Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Total kept	Total effort
1936	0	0	0	31	77	179	474	559	256	210	162	71	40	15	8	0	0	0	2082	3782
	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1937	0	7	0	4	22	148	490	808	429	159	29	11	0	7	0	0	0	0	2114	3865
	0	*0*	*0*	*119*	*204*	*204*	*86*	*14*	*5*	*0*	*0*	*0*	*0*						*632*	*1157*
1938	0	0	9	59	100	218	333	348	155	71	3	8	3	0	3	0	0	0	1310	2313
	0	*4*	*12*	*37*	*105*	*89*	*37*	*12*	*8*	*0*	*0*	*0*	*0*						*304*	*726*
1939	0	8	22	22	81	217	346	427	217	89	59	37	16	8	2	4	2	0	1557	2853
	0	*0*	*25*	*49*	*111*	*49*	*124*	*49*	*12*	*0*	*0*	*0*	*0*						*419*	*519*
1940	0	2	3	14	39	156	322	316	239	68	53	16	8	2	2	2	2	0	1244	1890
	0	*0*	*98*	*38*	*68*	*92*	*73*	*32*	*17*	*4*	*0*	*0*	*0*						*422*	*673*
1941	0	0	0	4	20	141	283	211	132	31	24	11	4	0	2	0	0	0	863	1613
	0	*0*	*29*	*118*	*75*	*64*	*136*	*25*	*47*	*7*	*0*	*0*	*0*						*501*	*921*
1942	0	2	0	5	14	72	153	117	93	38	20	2	0	2	2	0	0	0	520	964
	0	*0*	*6*	*90*	*90*	*12*	*15*	*3*	*15*	*0*	*0*	*0*	*0*						*231*	*362*
1943	0	0	0	0	23	87	276	151	121	36	21	4	0	0	0	0	0	0	719	1220
	0	*0*	*6*	*81*	*81*	*68*	*12*	*12*	*12*	*0*	*6*	*0*	*0*						*278*	*462*
1944	0	0	0	12	28	112	143	299	127	76	36	24	20	16	4	8	4	0	909	1611
	0	*0*	*35*	*76*	*157*	*127*	*56*	*20*	*5*	*0*	*0*	*0*	*0*						*476*	*600*
1945	0	0	0	3	7	105	298	348	254	78	61	41	27	20	3	10	0	0	1255	2274
	0	*0*	*15*	*255*	*170*	*116*	*85*	*39*	*15*	*0*	*8*	*0*	*0*						*703*	*1615*
1946	0	0	0	3	10	118	332	224	239	30	20	20	5	5	0	0	0	0	1006	2414
	0	*0*	*62*	*152*	*346*	*133*	*92*	*53*	*40*	*13*	*7*	*5*	*0*						*903*	*1545*
1947	0	0	0	4	16	88	162	247	106	35	23	14	5	4	2	0	0	0	706	1960
	0	*0*	*166*	*174*	*178*	*145*	*60*	*42*	*23*	*17*	*6*	*4*	*2*						*817*	*1612*
1948	0	0	2	3	37	182	262	269	146	26	16	18	6	5	5	0	0	0	977	2583
	0	*4*	*69*	*500*	*144*	*39*	*55*	*23*	*9*	*5*	*0*	*2*	*0*						*850*	*1487*
1949	0	0	3	10	27	105	261	308	208	69	71	30	18	7	4	5	1	0	1127	2868
	0	*2*	*136*	*292*	*531*	*186*	*54*	*31*	*17*	*4*	*0*	*2*	*0*						*1255*	*2198*
1950	0	0	0	3	78	238	305	312	251	73	60	33	10	5	3	1	0	0	1372	4276
	0	*8*	*309*	*640*	*241*	*181*	*38*	*23*	*15*	*0*	*0*	*0*	*0*						*1455*	*3956*
1951	0	0	0	0	5	72	217	354	287	89	71	64	27	13	7	4	0	0	1210	4041
	0	*0*	*72*	*442*	*168*	*57*	*42*	*4*	*0*	*11*	*0*	*0*	*0*						*796*	*1986*
1952	0	0	0	0	10	61	185	263	245	95	90	54	19	7	0	7	0	0	1036	3063
	0	*0*	*28*	*113*	*286*	*102*	*50*	*12*	*9*	*2*	*2*	*0*	*0*						*604*	*1291*
1953	0	0	1	1	20	86	213	236	166	57	50	23	4	4	1	0	0	0	862	2956
	0	*0*	*14*	*330*	*173*	*142*	*27*	*0*	*6*	*4*	*0*	*0*	*0*						*696*	*1181*
1954	0	0	0	13	39	140	225	403	206	110	61	19	15	12	3	1	1	0	1248	5331
	0	*0*	*11*	*19*	*452*	*109*	*121*	*15*	*6*	*0*	*0*	*0*	*0*						*733*	*2221*
1955	0	0	0	6	58	128	196	236	195	73	75	40	14	10	0	1	0	0	1032	4278
	0	*5*	*274*	*124*	*80*	*411*	*96*	*75*	*18*	*13*	*0*	*0*	*0*						*1096*	*2542*
1956	0	0	1	21	106	201	194	185	114	55	34	21	8	4	0	0	0	0	944	4392
	0	*3*	*135*	*520*	*71*	*77*	*108*	*11*	*14*	*0*	*0*	*0*	*0*						*939*	*2869*
1957	0	0	1	22	126	262	259	310	206	97	49	51	31	11	5	3	0	0	1433	5442
	0	*27*	*38*	*170*	*236*	*22*	*11*	*23*	*4*	*4*	*0*	*0*	*0*						*535*	*944*
1958	0	1	4	12	95	236	223	341	224	106	60	42	18	18	7	6	0	1	1394	7433
	2	*0*	*237*	*30*	*158*	*105*	*8*	*10*	*20*	*2*	*2*	*0*	*0*						*574*	*2291*
1959	0	0	1	6	33	116	118	257	162	94	52	33	17	7	1	0	0	0	897	5053
	0	*2*	*43*	*835*	*52*	*59*	*24*	*0*	*2*	*2*	*0*	*0*	*0*						*1019*	*2395*
1960	0	0	1	22	39	62	54	159	106	67	31	34	16	10	7	0	0	0	608	4217
	36	*36*	*107*	*27*	*642*	*36*	*27*	*6*	*6*	*0*	*9*	*0*	*0*						*932*	*2281*

TABLE 2. (*Concluded*)

Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Total kept	Total effort
1961	0	0	6	17	35	78	53	106	87	48	28	17	10	3	0	1	0	0	489	2940
	2	*34*	*43*	*101*	*13*	*389*	*9*	*11*	*2*	*2*	*0*	*0*	*0*						*606*	*1605*
1962	0	0	2	46	95	115	143	97	119	56	24	2	2	2	2	0	0	0	705	3706
	8	*20*	*541*	*68*	*84*	*6*	*163*	*4*	*10*	*4*	*0*	*8*	*0*						*916*	*1654*
1963	0	0	6	25	94	154	144	97	86	42	28	11	2	5	0	0	0	0	694	3784
	11	*162*	*191*	*1007*	*47*	*65*	*29*	*74*	*4*	*2*	*0*	*0*	*0*						*1592*	*3398*
1964	0	3	10	65	200	282	227	190	114	73	79	58	24	10	4	1	0	0	1340	6518
	0	*73*	*847*	*278*	*302*	*60*	*30*	*18*	*30*	*0*	*0*	*0*	*0*						*1638*	*3704*
1965	0	0	3	18	84	171	182	163	98	70	67	46	41	15	5	0	1	0	964	5788
	0	*2*	*70*	*463*	*70*	*85*	*5*	*5*	*2*	*3*	*0*	*2*	*0*						*707*	*1369*
1966	0	0	5	20	55	114	132	184	112	61	59	54	26	24	9	7	0	1	863	5381
	0	*0*	*14*	*251*	*613*	*61*	*136*	*0*	*0*	*4*	*0*	*0*	*0*						*1079*	*1719*
1967	0	0	4	45	117	171	116	121	92	31	23	23	30	16	13	1	3	0	806	4756
	0	*0*	*41*	*238*	*352*	*394*	*93*	*31*	*5*	*5*	*0*	*0*	*0*						*1159*	*2234*
1968	0	0	1	41	229	318	183	145	91	43	38	22	16	9	11	9	2	1	1159	5821
	0	*2*	*2*	*102*	*230*	*230*	*66*	*5*	*3*	*0*	*0*	*0*	*0*						*640*	*1213*
1969	0	0	7	23	80	177	240	176	87	43	62	54	43	36	22	15	6	2	1073	6819
	0	*1*	*126*	*85*	*210*	*225*	*156*	*53*	*15*	*3*	*3*	*1*	*0*						*878*	*2337*
1970	1	0	13	74	94	109	116	117	100	62	58	44	40	41	19	13	8	3	912	6087
	0	*8*	*141*	*391*	*193*	*263*	*126*	*153*	*90*	*20*	*3*	*0*	*0*						*1388*	*2857*
1971	0	0	27	130	280	303	193	106	142	52	72	51	51	32	19	13	5	3	1479	7710
	0	*20*	*61*	*165*	*390*	*92*	*250*	*31*	*77*	*19*	*3*	*3*	*3*						*1114*	*2087*
1972	0	0	21	133	289	254	199	131	96	49	46	51	33	28	12	8	4	1	1355	6398
	0	*31*	*222*	*155*	*237*	*174*	*48*	*22*	*19*	*15*	*2*	*2*	*0*						*927*	*2716*
1973	0	0	41	158	505	396	395	300	140	69	42	56	50	45	4	9	4	3	2217	9515
	12	*80*	*436*	*905*	*460*	*193*	*73*	*26*	*5*	*7*	*2*	*0*	*0*						*2199*	*5505*
1974	1	0	25	100	275	409	378	301	192	95	48	50	37	17	6	6	3	0	1943	9775
	0	*22*	*358*	*565*	*348*	*109*	*47*	*12*	*5*	*2*	*0*	*0*	*0*						*1468*	*3295*
1975	0	0	23	86	155	214	198	256	158	53	48	43	29	16	3	4	0	0	1286	7599
	9	*54*	*202*	*605*	*490*	*268*	*32*	*16*	*9*	*2*	*0*	*2*	*0*						*1689*	*4324*
1976	0	8	29	121	211	240	260	328	181	85	75	58	44	12	10	4	1	0	1667	8843
	0	*24*	*253*	*108*	*637*	*271*	*194*	*20*	*24*	*8*	*5*	*5*	*2*						*1551*	*3636*
1977	0	0	32	91	253	328	208	213	151	87	70	57	30	8	5	1	0	1	1535	8480
	0	*64*	*34*	*687*	*130*	*261*	*186*	*153*	*6*	*3*	*6*	*0*	*0*						*1530*	*2854*
1978	0	0	29	164	304	347	329	229	156	106	61	57	25	13	7	1	3	1	1832	9420
	0	*16*	*117*	*110*	*637*	*58*	*80*	*54*	*39*	*4*	*5*	*0*	*0*						*1120*	*3039*
1979	0	1	26	166	446	431	348	270	180	100	40	35	20	8	5	4	1	1	2082	10 705
	0	*0*	*61*	*395*	*149*	*561*	*53*	*35*	*9*	*18*	*0*	*0*	*0*						*1281*	*3807*
1980	0	2	51	187	334	427	349	303	263	123	62	42	17	14	2	9	1	1	2187	12 522
	0	*0*	*0*	*217*	*330*	*151*	*208*	*19*	*19*	*0*	*0*	*0*	*0*						*944*	*2699*
1981	0	1	16	153	329	345	233	203	203	132	66	47	30	11	7	0	2	0	1778	11 509
	0	*6*	*24*	*42*	*255*	*230*	*18*	*36*	*0*	*0*	*0*	*0*	*0*						*611*	*1272*
1982	0	0	4	76	334	316	294	189	222	109	65	33	19	15	8	8	1	0	1693	11 220
	0	*0*	*10*	*97*	*40*	*140*	*80*	*20*	*13*	*3*	*0*	*0*	*0*						*403*	*1136*
1983	0	2	25	57	224	342	288	194	242	143	66	40	30	12	12	3	2	0	1682	10 213
	0	*4*	*37*	*110*	*263*	*129*	*91*	*62*	*30*	*10*	*1*								*737*	*2090*

we obtained annual estimates of the instantaneous total mortality rate (Z, per year) for those age groups fully recruited to the fishery. Then, we estimated the instantaneous natural mortality rate (M, per year) from linear regressions of Z on effort and used this value of M to obtain estimates of the instantaneous fishing mortality rate (F, per year) for each year using separable virtual population analysis (SVPA, Pope and Shepherd 1982). With estimates of M and annual estimates of F for each population, mark–recapture data were used to estimate changes in survey effectiveness. These estimates were then applied to the recorded catch figures to obtain annual estimates of total catch from each fishery. Finally, annual estimates of abundance for each

population were obtained by applying both SVPA and VPA (virtual population analysis, Sims 1982) to the total catch at age data. These abundance estimates were then checked against independent estimates obtained from mark–recapture experiments.

Estimating the Components of Mortality

Catch curves, by age, were derived for different segments of the time series and compared. In each case, the descending right limb of the catch curve was quite straight, indicating that older fish were equally vulnerable to the fishery (Ricker 1975). The first age group to the right of the catch curve peak was taken to be the youngest age group fully recruited to the fishery. For lake trout, fish aged 8 and over were fully and equally vulnerable to the fishery throughout the period from 1936 to 1983. For smallmouth bass, fish aged 5 and over remained fully vulnerable throughout. For each population, several estimates of Z for the stock of fully vulnerable fish were calculated for each year. Estimates of Z were obtained from the catch-at-age data alone, using virtual population statistics (Z_{BIO} from the biostatistical rate of exploitation, Ricker 1975, p. 184), and from the catch-per-effort data. The creel survey provides several measures of annual fishing effort: total effort (angler hours, EFT) exerted by parties fishing for a particular species (see Fig. 1; the percentage of anglers that fish for both species is low — their total effort is split equally between the two species); total effort exerted by parties who caught at least one representative of the species sought (EFC1); total effort exerted by parties who caught and kept at least one representative of the species sought (EFK1: see Table 2). For smallmouth bass, these measures of effort differ markedly. For lake trout, they are relatively similar. Estimates of Z were obtained using each of these three measures of effort (Z_{EFT}, Z_{EFC1}, Z_{EFK1}, respectively).

The effort-based Z estimates were much more variable than the biostatistical estimates, but all three exhibited significant ($P < 0.05$) positive correlations with the biostatistical estimates (Table 3). Overall, Z_{EFK1} values exhibited the greatest degree of similarity with the Z_{BIO} values (Table 3). We chose to rely on the biostatistical estimates of Z because they are independent of changes in angler effectiveness and relatively insensitive to moderate, year-to-year variations in survey coverage and fishing intensity (Bishop 1959; Ricker 1971). However, these estimates are based on virtual population statistics, and therefore, large variations in fishing intensity subsequent to a particular year can introduce a significant bias into the estimate for that year. Bishop (1959) developed equations for assessing the magnitude of this bias, when the value for M is known.

Preliminary estimates of M for each species ($M_{trout} = 0.12$, $M_{bass} = 0.26$) were derived from Pauly's (1980) regression equation:

$$\log_{10} M = -0.0066 - 0.279 \log_{10} L_\infty + 0.6543 \log_{10} K + 0.463 \log_{10} \bar{T}$$

where L_∞ and K are the von Bertalanffy growth parameters and $\bar{T}$ is the annual mean temperature of the water in which the stock lives. Estimates for L_∞ and K (trout: 96 cm, 0.08, respectively; bass: 50 cm, 0.15, respectively) were obtained from the mean length at age data provided by the creel survey. Estimates for $\bar{T}$ (trout: 5.9°C; bass: 8.8°C) were derived from extensive data on the annual water temperature cycle in Lake Opeongo. In calculating $\bar{T}$, we assumed that smallmouth bass remain in the epilimnion during summer stratification (Coble 1975), while lake trout remain in the hypolimnion (Martin and Olver 1980). We used these values for M in Bishop's (1959) equations to estimate, and then correct for, biases present in the biostatistical estimates of Z. Overall, these biases appeared to be relatively small. The averages of the absolute values of the estimated bias terms in the lake trout and smallmouth bass Z_{BIO} values were 0.02 and 0.08, respectively.

TABLE 3. Parametric (Pearson) and nonparametric (Spearman) correlations between annual estimates of total mortality rate based on the biostatistical rate of exploitation (Z_{BIO}) and annual total mortality rate estimates based on the following catch-per-unit-effort statistics: TK/EFT, TK/EFC1, TK/EFK1 where TK is the total reported number of fish of the relevant species kept by anglers, EFT is the total reported effort (angler-hours) directed against the relevant species, EFC1 is the total effort (angler-hours) reported by parties that caught at least one fish belonging to the relevant species, and EFK1 is the total effort (angler-hours) reported by parties that kept at least one fish belonging to the relevant species. The smallmouth bass (SMB) correlations are based on 41 yr of data; the lake trout (LT) correlations are based on 40 yr of data. All coefficients are statistically significant ($P < 0.05$).

			Effort-based Z estimates		
Species			Z_{EFT}	Z_{EFC1}	Z_{EFK1}
SMB	Z_{BIO}	Parametric	0.439	0.481	0.516
		Nonparametric	0.385	0.438	0.489
LT	Z_{BIO}	Parametric	0.472	0.465	0.462
		Nonparametric	0.419	0.409	0.421

Refined estimates of M were obtained using a method based on the following equation (Paloheimo 1961, 1980):

$$Z = M + F = M + qE$$

where q is the catchability coefficient and E is a measure of fishing effort. We carried out a regression analysis of the dependence of the corrected Z_{BIO} values on EFK1 for each population. We chose EFK1 as our measure of effort because the Z estimates based on EFK1 exhibited the greatest degree of similarity with our initial Z_{BIO} estimates (Table 3). The regression analysis for each population revealed the same basic pattern: a weak ($r \sim 0.40$) but significant ($P < 0.05$) dependence overall and a strong ($r \sim 0.70$) dependence in both the early and late segments of the time series, with the slope of the relation holding in the early part of the time series significantly ($P < 0.05$) greater than the slope of the relation holding in the later part of the time series. For both species, M was estimated using a weighted average of the intercept estimates for the two Z_{BIO}–EFK1 geometric mean regressions (lake trout, estimate with 95% confidence interval: $M_{early} = -0.11 \pm 0.30$, $M_{late} = 0.12 \pm 0.06$; smallmouth bass: $M_{early} = 0.29 \pm 0.13$, $M_{late} = 0.33 \pm 0.19$). For lake trout, the final estimate for M was 0.11 ± 0.06. For smallmouth bass, it was 0.30 ± 0.11.

The analysis outlined above demonstrated that the time series for each species could be divided into three segments (1936–47, 1948–63, 1964–83) such that a strong dependence of Z on EFK1 would hold in the first and last segments. With this in mind, we applied the SVPA procedure of Pope and Shepherd (1982) to the catch-at-age data for fully catchable fish (LT: ≥ 8; SMB: ages ≥ 5) to refine our annual estimates of F for each species. The SVPA procedure requires that the user define the

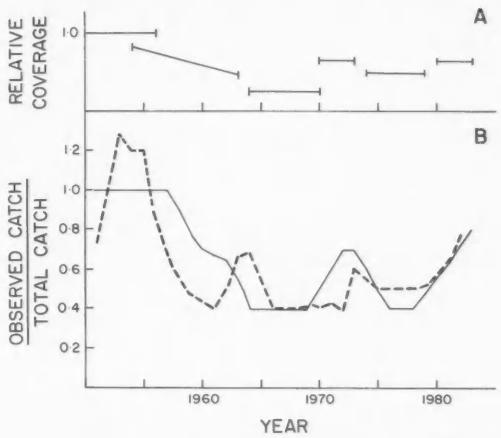

FIG. 4. Schematic summary of opinion, provided by those responsible for directing the creel survey, on changes in survey effectiveness over the period 1950–83. (B) Estimates of survey effectiveness (broken line) obtained by averaging annual estimates for both species and then smoothing using 3-yr running averages. The solid line gives the set of values for effectiveness used in deriving the final abundance estimates for both species (Fig. 5).

following parameters before application: M; F in final year of time series; range of ages considered; vulnerability of the oldest age group, relative to the vulnerability of a reference age group chosen arbitrarily near the middle of the range of ages considered. It then applies a least squares procedure to estimate relative vulnerability of all age groups considered, F for fully vulnerable age groups in each year, and abundance for each age group in each year. We applied it to the catch at age data for each species as follows: (1) M set equal to the species specific values listed above; (2) F for 1983 adjusted to maximize the correlation between F estimates and EFK1 over the final 20-yr segment (1964–83) of the time series (Pope 1983); (3) relative vulnerability of last age group (LT: age 12; SMB: age 8) set to insure that ages 8 and over, for lake trout, and ages 5 and over, for smallmouth bass, are assumed to be fully and equally vulnerable to the fishery.

The results of these initial SVPAs were similar for both lake trout and smallmouth bass: the dependence of F on EFK1 is strong in both the first and last segments of the time series, with relationships tighter for lake trout than for smallmouth bass; catchability declines rapidly in the middle segment of the time series, with the decline proceeding more smoothly for lake trout than for smallmouth bass.

Estimating Changes in Survey Effectiveness

Up until about 1950, there are good reasons for assuming that the catch recorded by the survey was essentially equal to total catch (McMurtry and Shuter 1985). After 1950, changes in both survey design and the fishery itself render this assumption invalid. The opinions of the survey managers on both the timing and relative magnitudes of changes in survey effectiveness (measured as recorded catch/total catch) are summarized in Fig. 4A. Gradual, unrecognized changes in effectiveness will not seriously affect SVPA estimates of F, but will totally invalidate SVPA estimates of absolute abundance. To obtain accurate population abundance estimates from the SVPA procedure, annual estimates of total catch-at-age must be available. We attempted to estimate and then correct for changes in survey effectiveness using both an indirect and a direct method.

The indirect method made use of data collected from the mark–recapture experiments on live fish. For years in which such experiments were performed, the total number of tags caught was estimated from the number of tags released and the appropriate F and M estimates for the year and species concerned. Survey effectiveness was then estimated as the number of tags recorded in the surveyed catch divided by the estimated total number of tags caught.

The direct method involved a procedure developed by Regier (1971) designed explicitly to evaluate the effectiveness of the Opeongo survey. This procedure involved a second angler interview program, run independently of the regular creel survey. Fishermen were interviewed on the lake, before completion of their fishing trips. Fish caught and in the possession of the fishermen were marked. The number of fish marked in this way was then compared with the number of these marks recorded by the regular survey. This was done for both species in 1969 and 1970 and for smallmouth bass alone in 1971 and 1972.

By pooling annual estimates of effectiveness for both species, and averaging estimates in years where there were more than one, we compiled a series of annual effectiveness estimates for 26 (missing years: 1954, 1957, 1958, 1961, 1967, 1968, 1974, 1975) of the 34 yr between 1950 and 1983 (Fig. 4B). The results are broadly consistent with the intuitive estimates of the survey managers: survey effectiveness was high from 1950 through to around 1955; declined irregularly to a low level in the 1960s; rose and fell in the early to mid-1970s; and rose again in the 1980s.

Estimating Population Abundance

The gross temporal trends in both the qualitative (Fig. 4A) and quantitative (Fig. 4B) estimates of survey effectiveness were simplified into a single scheme (Fig. 4B), and the total catch-at-age figures for both species were then adjusted to account for these changes. The set of SVPAs used to obtain annual estimates of F were then repeated using the adjusted catch at age data. The resultant estimates of total abundance for fully catchable age groups were then compared with independent abundance estimates derived from mark–recapture experiments. By making minor adjustments (Fig. 4B) to the effectiveness estimates, good agreement between these two methods for estimating abundance was obtained (Fig. 5).

The mark–recapture abundance estimates were generated by treating the creel survey as the sole source of recapture information. Since these same recaptures were used to estimate survey effectiveness, there is some possibility of a subtle statistical linkage between the mark–recapture and SVPA abundance estimates. In the years 1976–81, recapture data from an independent trap netting program were also used to estimate abundance. The estimates obtained from both recapture methods were similar (Table 4). This agreement increased our confidence in the reliability of both the mark–recapture and the SVPA abundance estimates for fully catchable fish.

Abundance estimates for partially recruited age groups (LT: ages ≤ 7; SMB: ages ≤ 4) were obtained by applying simple VPA (Sims 1982) to the catch data from individual cohorts. In applying VPA, only catch data from partially recruited ages were used. Values for M were the same as those used in the SVPAs of fully catchable age groups. The VPA for each cohort

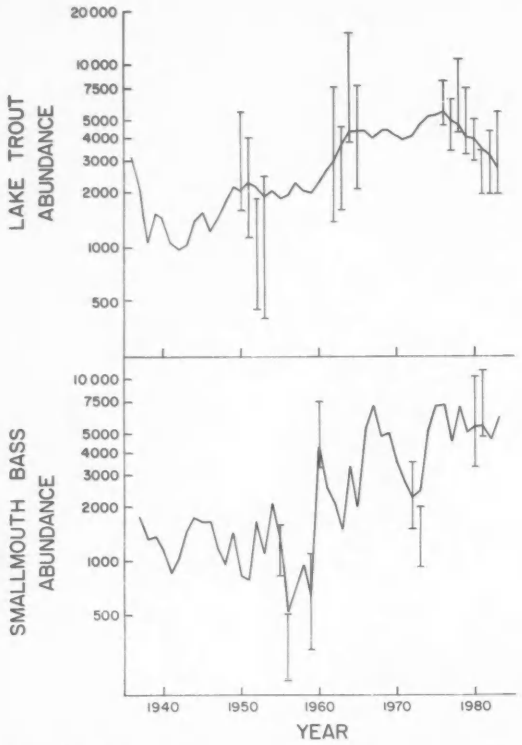

FIG. 5. Changes in the abundance of lake trout and smallmouth bass over the period 1936–83. The lines connect annual estimates obtained from separable virtual population analyses of each species. The vertical bars give 95% confidence intervals for mark–recapture population estimates in those years where such estimates can be made. All estimates are for that segment of each population which is fully vulnerable to the angling fishery: lake trout — ages ≥ 8; smallmouth bass — ages ≥ 5.

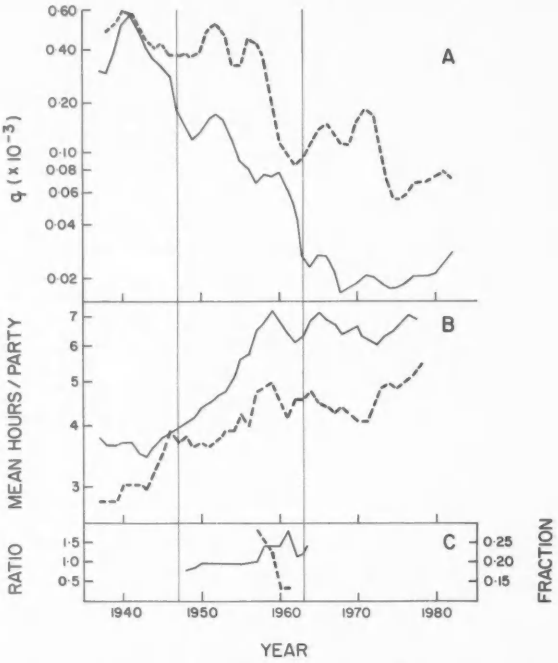

FIG. 6. (A) Changes in the catchability coefficient for lake trout (solid line) and smallmouth bass (broken line) over the period 1936–83; data smoothed using 3-yr running averages. (B) Changes in the average number of hours a party spent fishing for lake trout (solid line) and for smallmouth bass (broken line); data smoothed using 3-yr running averages. (C) Changes in the fraction of parties which are guided (broken line) and in the ratio (average catch-per-unit-effort guided parties):(average catch-per-unit-effort all parties). Estimates of the first quantity are available for 1957–61 inclusive; estimates of the second are available for 1948–50, 1955, and 1957–64. Results from both species have been averaged.

TABLE 4. Comparison of independent population estimates from tag recaptures obtained through the creel survey and from tag recaptures obtained from trap netting.

Year	Species	N (95% C.I.) Creel	N (95% C.I.) Trap	N_{creel}/N_{trap}
1976	LT	6137 (4731–8209)	5081 (3968–6733)	1.21
1977	LT	4665 (3419–6543)	5100 (3531–7651)	0.91
1978	LT	6732 (4351–10 933)	5624 (3323–10 152)	1.20
1979	LT	4823 (3243–7496)	3714 (1990–7563)	1.30
1980	SMB	5753 (3340–10 389)	4186 (3298–5758)	1.37
1981	SMB	7250 (4915–11 154)	6615 (4410–10 395)	1.09

was initiated by using, as input, the SVPA abundance estimate for the youngest, fully catchable age group (LT: age 8; SMB: age 5) of the cohort. The SVPA and VPA results together provide a consistent series of estimates which show how the absolute abundance of each cohort changed during the period that it was subject to exploitation.

Estimating and Evaluating Changes in Catchability

The final SVPA estimates of F, based on our best estimates of total catch-at-age, suggested that the catchability of both species declined considerably over the period from the 1940s through to the early 1960s (Fig. 6A). For lake trout, the decline was rapid but irregular and was followed by a period of relative stability (1965–82). For smallmouth bass, a period of slow irregular decline (1937–57) was followed by a rapid drop (1958–62) and then a further period of very irregular decline (1963–82). At least some of these changes in catchability can be explained by coincident changes in the fishery itself.

If we compare, within a year, the catch-per-unit-effort of parties which spend varying amounts of time fishing (Table 5), we find much higher values among parties that fish for shorter periods of time. If we then examine the extent to which the average duration of a fishing trip has changed over the interval

TABLE 5. Comparisons of relative catch-per-unit-effort for parties that spend different amounts of time fishing. Values within each year were divided by the value for the shortest trips; yearly values were then averaged over the designated time intervals. The values provide a direct measure of the decline in effectiveness of 1 angler-hour as the length of the fishing trip increases.

Duration of trip (h)	Lake trout		Smallmouth bass	
	1936–47	1964–79	1936–47	1964–79
0–2.5	1.00	1.00	1.00	1.00
2.5–4.5	0.54	0.53	0.58	0.55
4.5–6.5	0.38	0.40	0.30	0.41
6.5–8.5	0.27	0.31	0.25	0.28
8.5–10.5	0.21	0.27	0.12	0.28
10.5–12.5	0.23	0.23	—	0.25
12.5–14.5	—	0.18	—	0.18
14.5–16.5	—	0.18	—	0.13
>16.5	—	0.15	—	0.10

1936–83 (Fig. 6B), we see a long and continuous increase, for both species, beginning around 1945 and ending around 1956. The timing of this increase in the duration of an average trip is roughly coincident with the initial catchability decline for both species. For lake trout, a shift in trip duration from about 3.6 h (the value for 1936–45) to about 6.5 h (the value for 1957–83) would lead to a decline in catchability of at least 40% (i.e. calculated from the frequency distribution for trip duration in each time period and the relationship between effort effectiveness and trip duration illustrated in Table 5).

Another major change in the fishery in the 1950s and 1960s was the gradual disappearance of guides. Data on the relative effectiveness and extent of guiding are sporadically available over the period 1948–64 (Fig. 6C). For those years (1957–64) when meaningful comparisons between guided and nonguided parties could be made, we found that the average ratio of catch-per-unit-effort figures (nonguided versus guided parties) was similar for both species, with a value around 0.65. The effectiveness of guided parties is essentially equal to that of all parties combined (Fig. 6C) up to 1957; then it increases and remains at a higher level until 1964. Over the 5 yr (1957–61) for which the extent of guiding can be determined directly, we see (Fig. 6C) a sudden drop in 1960 (coincident with the closing of the lodge) from a value over 20% to a value around 10%. Taken together, these results suggest that (1) guided parties were more effective than nonguided parties, (2) most parties were guided up until 1957 because the overall effectiveness of the average party was equivalent to that of guided parties up until that point in time, and (3) the extent of guiding began to decline in 1958 and had reached a low level by 1960. The timing of these changes in the extent of guiding is roughly coincident with both the late 1950s catchability decline for smallmouth bass and the final phase of the long catchability decline for lake trout. If the fishery did change from completely guided to completely unguided, we would expect a decline in the catchability coefficient of at least 35% (i.e. this follows from the fact that nonguided effort was estimated to be 65% as effective as guided effort).

The changes in the fishery, discussed above, would lead to an overall reduction in the catchability coefficient of about 60% (i.e. the combined effect of trip extension and loss of guides is to reduce the effectiveness of one unit of effort to $0.60 \times 0.65 = 0.39$ of its former value: a reduction in catchability of about 60%) for both species. The observed reduction is about 95% for lake trout and about 80% for smallmouth bass.

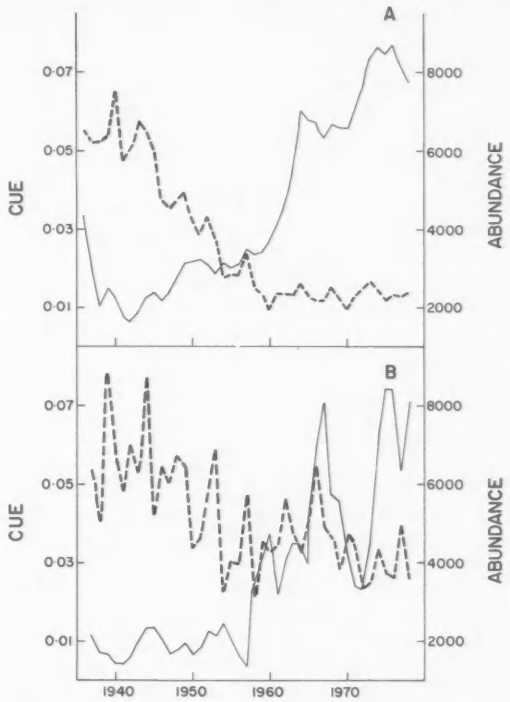

FIG. 7. Comparison of catch-per-unit-effort (CUE, broken line) and abundance (solid line) for (A) lake trout and (B) smallmouth bass. CUE is the total number of fish kept by anglers divided by the total effort directed against the species. Abundance is the SVPA–VPA estimate of the total number of fish vulnerable to the fishery. For each age group partially recruited to the fishery, a fraction of the total number was assumed to be vulnerable: that fraction was estimated by dividing the VPA estimate of F for the age group by the SVPA estimate of F for fully vulnerable fish.

Discussion

The primary objective of a creel survey is to provide reliable information on population abundance and fishing pressure. Our analyses of the Lake Opeongo creel survey lead to a number of conclusions on reliability which closely parallel conclusions derived from studies of commercially exploited marine stocks (Saville 1980). We have shown that simple measures of population abundance and fishing pressure, based on catch and effort data, can be useful for restricted periods of time. However, we have also shown that angling fisheries can change rapidly and that failure to account for such changes will lead to a grossly distorted picture of both the status of the population and the impact of the fishery on it. For both Opeongo populations, long-term changes in overall catch-per-unit-effort were of no value whatsoever in describing long-term changes in the abundance of catchable fish (Fig. 7).

Changes in the character of the fishery can be monitored directly by insuring that the creel survey is designed to keep track of the relative contribution and effectiveness of identifiable groups of anglers with different "skill" levels. Such

information can be used to predict changes in average catchability, arising from demographic shifts in the angling population. The survey data themselves can then be adjusted to take account of such shifts. Various techniques for handling this situation have been developed in marine fisheries (Kimura 1981). However, changes in catchability can arise from changes in the population itself (Paloheimo and Dickie 1964; Winters and Wheeler 1985). The timing and extent of such changes cannot be reliably monitored with samples of catch and effort data alone. Measures of relative abundance and fishing pressure that are independent of effort data are required. Two classes of methods provide this kind of information: cohort analysis procedures and mark–recapture experiments.

Cohort analysis procedures can function with creel survey data alone, but to be used effectively, such methods require (1) a relatively long (~10 yr) and uninterrupted time series of reliable estimates of relative catch-at-age and (2) constant survey effectiveness throughout the time series or known, and accounted for, changes in effectiveness. Reliable estimates of abundance and mortality, for the latter part of the time series, require an independent estimate of fishing mortality, or abundance, in the most recent year. Mark–recapture experiments can provide reliable estimates of abundance levels and mortality rates. They can also provide reliable estimates of survey effectiveness (Regier 1971). Our analyses could not have been carried out to the depth presented without the mark–recapture data, since these permitted the gaps in the survey data to be filled and the uncertainties checked. By integrating both methods into an overall study design, the weaknesses of each can be circumvented.

Our experience indicates that long-term creel surveys can only be expected to provide reliable information if they form part of a broader study design which includes periodic, independent assessment of the status of the population, the fishery, and the survey itself. Mark–recapture experiments and frame surveys (Bazigos 1974) can be used for such assessments. There may be other techniques which are equally effective. The important point is that such assessments should be done periodically as a matter of course. Data generated internally by a creel survey can indicate that significant changes in the fishery may be occurring, but independent assessment is required to determine the extent and importance of those changes. A major objective of study design should be to attain optimal integration between data provided by the creel survey and data provided by independent assessment.

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Evaluation of the Effects of Fish Community Structure on Observed Yields of Lake Trout (*Salvelinus namaycush*)[1]

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Creel and lake survey data from 87 Ontario lakes with self-sustaining lake trout (*Salvelinus namaycush*) populations were analysed to determine the effect of intrinsic factors, such as fish community structure, and extrinsic factors, such as angling-effort, on the observed yields of lake trout. Multiple regression analyses showed that angling-effort and lake area, in order of importance, explained almost 82% of the variation in annual catches. Analyses of covariance were used to test a variety of hypotheses about how community structure — the presence of forage, competitors, or alternate sports species — affected the catch of lake trout. No significant differences among groups were detected, which suggests that fish community structure has little or no effect on actual yield of lake trout. The difficulties inherent in using catch and effort data alone to evaluate the importance of factors affecting productivity (or potential yield) are discussed.

Les auteurs ont analysé les données recueillies au cours d'enquêtes sur la pêche sportive et de relevés de 87 lacs ontariens fréquentés par des populations autonomes de touladi (*Salvelinus namaycush*) afin de déterminer l'incidence de facteurs intrinsèques, dont la structure de la communauté des poissons, et de facteurs extrinsèques, dont l'effort de pêche à la ligne, sur les rendements observés du touladi. Des analyses de régression multiple ont révélé que l'effort de pêche et la superficie du lac, dans cet ordre, sont liés à près de 82 % de la variation des prises annuelles. Les auteurs ont utilisé des analyses de la covariance pour vérifier une variété d'hypothèses sur la manière dont la structure de la communauté (présence de poissons de fourrage, compétiteurs ou autres espèces de pêche sportive) influe sur les captures de touladi. Aucune différence significative n'a été notée entre les groupes, ce qui porte à croire que la structure de la communauté n'a guère d'incidence sur le rendement effectif du touladi. Les auteurs étudient les problèmes qui se posent lorsqu'on utilise seulement des données sur l'effort et les prises pour évaleur l'importance de facteurs influant sur la productivité (ou le rendement potentiel).

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Ryder (1965) developed the morphoedaphic index (MEI) as a first-order predictor of potential fish production ("sustainable" yield) at the fish community level. It has become standard fisheries management practice in Ontario to use the Ryder equation, expressed in metric units ($Y = 1.4\text{MEI}^{0.45}$ where Y = yield in kilograms per hectare) to estimate potential fish production for lakes. Thus, managers are able to relate the actual (observed) yield to the potential yield for a particular lake, as a first-order estimate of the intensity of exploitation. Interpretation of this relationship should be viewed with caution, however, particularly if the stage of development of the fishery is not known. Because of its questionable precision, other indicators, in addition to yield, are needed to assess exploitation accurately (Ontario Ministry of Natural Resources (OMNR) 1983).

Recently, an attempt was made to partition the potential fish

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TABLE 1. Physical, chemical, and catch and effort data for 87 Ontario lake trout lakes.

Lake name	Area (ha)	Mean depth (m)	TDS	MEI	Lake trout catch ($kg \cdot yr^{-1}$) Yield ($kg \cdot ha^{-1} \cdot yr^{-1}$)	Angler-hours (yr^{-1}) Effort ($h \cdot ha^{-1} \cdot yr^{-1}$)
Adelaide	137	12.8	28.0	2.1	274.00 2.00	2219.40 16.20
Aegean	482	10.3	15.4	1.4	53.02 0.11	241.00 0.50
Aiabewatik	163	9.0	94.5	10.5	267.32 1.64	883.46 5.42
Anstruther	625	14.9	30.2	2.0	581.25 0.93	10 437.50 16.70
Aylen	2 016	27.2	41.9	1.5	907.20 0.45	9455.00 4.69
Birch	196	13.2	—	—	343.00 1.75	7175.56 36.61
Blue	177	6.7	31.0	1.1	70.84 0.44	1465.10 9.10
Bone	123	8.5	17.0	2.0	200.49 1.63	3530.10 28.70
Boshkung (1977)	716	23.1	34.6	1.4	1539.40 2.15	40 323.04 56.19
Cassels	772	9.7	58.2	6.0	324.24 0.42	— —
Chandos	115	6.2	21.6	3.4	13.80 0.12	586.50 5.10
Chiblow-Denman	2725	23.9	27.0	1.1	1629.42 0.78	10 862.80 5.20
Christman	57	8.8	30.0	3.4	76.38 1.34	627.00 11.00
Clear	187	20.4	50.0	2.4	471.24 2.52	3753.09 20.07
Clearwater	119	13.8	33.1	2.3	47.60 0.40	464.10 3.90
Cucumber	81	10.3	49.4	4.7	61.56 0.76	364.50 4.50
Cumming	71	7.9	37.9	4.7	5.68 0.08	— —
Dana	111	7.4	29.6	4.0	58.83 0.53	631.59 5.69
Darraugh	182	14.8	26.7	1.8	123.76 0.68	2531.62 13.91
Devil	1062	14.4	109.0	7.5	3674.52 3.46	27 601.38 25.99
Dickie	214	18.3	90.0	4.9	179.76 0.84	4686.60 21.90
Domain	550	7.4	19.2	2.5	22.00 0.04	280.50 0.51
Drag	912	20.1	42.2	2.0	282.72 0.31	6019.20 6.60
Eaglerock	168	12.9	45.0	3.4	159.60 0.95	1592.64 9.48
Eels	946	6.7	57.6	8.5	718.96 0.76	11 446.60 12.10
Elliot	616	15.6	82.7	5.3	486.64 0.79	3338.72 5.42

TABLE 1. (*Continued*)

Lake name	Area (ha)	Mean depth (m)	TDS	MEI	Lake trout catch ($kg \cdot yr^{-1}$) Yield ($kg \cdot ha^{-1} \cdot yr^{-1}$)	Angler-hours (yr^{-1}) Effort ($h \cdot ha^{-1} \cdot yr^{-1}$)
Emerald	567	18.5	53.6	2.8	754.11 0.33	15 932.70 28.10
Esson	245	10.8	71.3	6.6	1401.40 5.72	16 160.20 65.96
Flack	934	21.6	26.0	1.2	1279.58 1.37	7677.48 8.22
Gull	996	16.5	41.3	2.4	867.24 0.66	— —
Haliburton	1014	17.4	34.8	1.9	294.06 0.29	2940.06 2.90
Halls	539	28.3	35.0	1.2	506.66 0.94	20 384.98 37.82
Icarus	762	11.6	23.2	2.0	544.50 0.75	5067.48 6.98
Kashagawigamog	818	13.0	49.4	3.8	179.96 0.22	4744.40 5.80
Kawagama	2821	21.8	21.8	1.0	1692.60 0.60	17 997.98 6.38
Kawashegamuk	1836	14.0	94.0	6.7	844.56 0.46	3268.08 1.78
Kennewapekko	217	13.1	26.2	2.0	28.21 0.13	91.14 0.42
Kennisis	1417	23.5	32.6	1.3	63.72 2.36	548.10 20.30
Kimball	213	22.5	24.7	1.0	164.01 0.77	1882.92 8.84
Lake Joseph	5156	24.7	24.7	1.0	4485.72 0.87	27 172.12 5.27
Lake Lavielle	2428	14.4	41.8	2.9	995.48 0.41	9881.96 4.07
Lake Temagami	20 972	18.2	26.0	1.4	8808.24 0.42	75 499.20 3.60
Lauzon	2244	35.4	29.0	0.8	32.20 0.26	547.40 4.43
Lee	283	14.4	25.9	1.7	164.14 0.58	1431.98 5.06
Little Quirke	397	13.7	24.3	1.7	142.92 0.36	1588.00 4.00
Louisa	490	17.0	45.9	2.7	725.20 1.48	4860.80 9.92
Lower Bass	106	8.0	36.8	4.6	162.18 1.53	1420.40 13.40
Manitou	322	18.0	41.4	2.3	341.32 1.06	4263.28 13.24
McConnell	207	12.1	25.4	2.0	202.86 0.98	4264.20 20.60
Merchants	412	8.9	27.6	3.1	160.68 0.39	671.56 1.63
Mississauga	588	17.8	33.8	1.9	335.16 0.57	6162.24 10.48
Mountain	320	13.5	36.4	2.6	64.00 0.20	6972.80 21.79

TABLE 1. (*Continued*)

Lake name	Area (ha)	Mean depth (m)	TDS	MEI	Lake trout catch ($kg \cdot yr^{-1}$) Yield ($kg \cdot ha^{-1} \cdot yr^{-1}$)	Angler-hours (yr^{-1}) Effort ($h \cdot ha^{-1} \cdot yr^{-1}$)
Northern Light	6875	8.4	26.9	3.2	1168.75 0.17	7906.25 1.15
Noxheiatik	90	9.3	42.8	4.6	11.70 0.13	102.60 1.14
Nunikani	116	7.9	20.5	2.5	80.04 0.69	968.60 8.35
Obabika	3158	12.6	35.3	2.8	442.12 0.14	— —
Opeongo	5158	14.6	26.3	1.8	99.82 0.62	584.43 3.39
Pevensey	155	9.2	22.1	2.4	159.65 1.03	4237.70 27.34
Pineneedle	1039	19.3	21.7	1.1	363.65 0.35	893.54 0.86
Pond	23	11.5	20.7	1.8	5.52 0.24	189.75 8.25
Rabbit	2108	14.2	62.5	4.4	1054.00 0.50	— —
Ranger	2256	21.7	26.0	1.1	631.68 0.28	10 016.64 4.44
Rawlinson	234	11.1	13.3	1.1	133.38 0.57	517.14 2.21
Redstone	1194	21.9	73.0	3.3	1337.28 1.12	25 515.78 21.37
Salmon	148	13.3	59.0	4.4	762.20 5.15	3840.60 25.95
Sasakewi	126	11.3	79.1	7.0	234.36 1.86	1014.30 8.05
Scattergood	282	6.1	20.1	3.2	620.40 2.20	3536.28 12.54
Seggemak	170	9.4	41.4	4.4	212.50 1.25	872.10 5.13
Semiwhite	305	13.7	27.0	1.9	353.80 1.16	3324.50 10.90
Sherborne	252	9.5	23.8	2.5	128.52 0.51	1869.84 7.42
Smoke	608	16.2	35.6	2.1	948.48 1.56	5320.00 8.75
Spring	70	22.3	83.0	3.7	45.50 0.65	917.00 13.10
Stormy	2443	18.3	68.0	3.7	2858.31 1.17	7011.41 2.87
Sunshine	575	20.6	18.5	0.8	126.50 0.22	391.00 0.68
Telescope	829	8.4	21.0	2.5	0.00 0.00	215.54 0.26
Thunder	176	18.6	29.8	1.6	105.60 0.60	306.24 1.74
Turtleshell	161	27.4	31.0	1.1	127.17 0.79	1605.17 9.97
Twelve Mile	336	12.0	38.4	3.2	114.24 0.34	2654.40 7.90

TABLE 1. (*Concluded*)

Lake name	Area (ha)	Mean depth (m)	TDS	MEI	Lake trout catch ($kg \cdot yr^{-1}$) Yield ($kg \cdot ha^{-1} \cdot yr^{-1}$)	Angler-hours (yr^{-1}) Effort ($h \cdot ha^{-1} \cdot yr^{-1}$)
Upper Bass	122	7.1	38.3	5.3	13.42 0.11	— —
Upper Manitou	5158	17.1	50.0	2.9	3920.08 0.76	7118.04 1.38
Wakwekobi	2709	38.7	26.0	0.6	1219.05 0.45	7856.10 2.90
Wapageisi	1652	11.3	36.0	3.1	280.84 0.17	1090.32 0.66
Wawiagama	618	8.8	59.0	6.7	30.90 0.05	— —
Wawiashkashi	415	5.6	48.0	8.5	78.85 0.19	4336.75 10.45
Wollaston	368	9.4	161.8	17.2	172.96 0.47	4084.80 11.10
Wrist	326	18.3	14.6	0.7	107.58 0.33	286.88 0.88
Yorkston	351	11.0	29.7	2.7	673.92 1.92	5861.70 16.70
N	87	87.0	87.0	87.0	87.0	80.0
Mean	1055	14.9	40.2	3.2	648.70 0.90	6328.80 10.90
SD	2438	6.5	24.3	2.5	1211.70 1.00	10 681.60 11.80
Range	1383–3494	8.4–21.4	15.9–64.5	0.7–5.7	563.00–1860.40 0.10–1.90	4352.80–17 010.40 0.90–22.70

community yield derived from the MEI into individual species yields (OMNR 1982). For example, the sustainable or "allowable" yield of lake trout (*Salvelinus namaycush*) was estimated to be about 25% of the potential yield for all species. Yield, however, was not partitioned on a fish community basis. That is, allowable yields for a species were not assigned such that they might vary with changes in the species assemblage. Oglesby (1982) recommended that the relationship between fish community structure and yield should be determined.

Further, there is a perception among local managers in the OMNR that fish community structure can affect the sustainable (allowable) yields of individual species. This perception could be of particular relevance in multispecies communities if only a few species are actively sought (targeted) by recreational or commercial fisheries. Colby (1984) expressed the possibility that "energy entering the ecosystem may be channeled through the target species at the expense of other species." Presumably, this could increase the sustainable yield of the target species.

The purpose of the present paper is to determine the effect that fish community structure has on the actual lake trout yield and to assess the relative importance of other extrinsic (e.g. effort) and intrinsic (e.g. diet, area, number of target species, etc.) factors in explaining differences in actual lake trout yields among a set of 87 recreationally fished lakes in Ontario.

Methods

Creel survey data from 87 recreationally fished Ontario lakes containing lake trout were obtained from published and unpublished OMNR reports. Data of interest included total catch (kilograms) of all fish species by season and by year, total catch (kilograms) of lake trout by season and by year, annual and seasonal levels of fishing effort (angler-hours) for lake trout alone and for all species combined, and the contribution of planted lake trout to the total lake trout catch (percent by weight). Morphometric, limnological, and biological data for these lakes (Gazetteer name) were obtained from the Ontario Lake Inventory Database (OLIDB). Data included values for lake area (A, hectares), mean depth ($\bar{Z}$, metres), and total dissolved solids (TDS, milligrams per litre). In addition, presence–absence information about the following species was also obtained: lake herring (*Coregonus artedii*); lake whitefish (*C. clupeaformis*); brook trout (*Salvelinus fontinalis*); rainbow smelt (*Osmerus mordax*); northern pike (*Esox lucius*); burbot (*Lota lota*); smallmouth bass (*Micropterus dolomieui*); yellow perch (*Perca flavescens*); and walleye (*Stizostedion vitreum*).

Initially, hundreds of creel reports were examined. Considerable editing of the database was required before analysis. Lakes were excluded from the database if they fell into one of the following categories: (a) no accurate estimate of *annual* lake trout catch available; (b) stocked lake trout were a significant component of the catch.

The number of annual catch and effort estimates per lake varied from 1 yr (the most common situation) to 45 yr. To insure that the precision of the estimates for all lakes was comparable

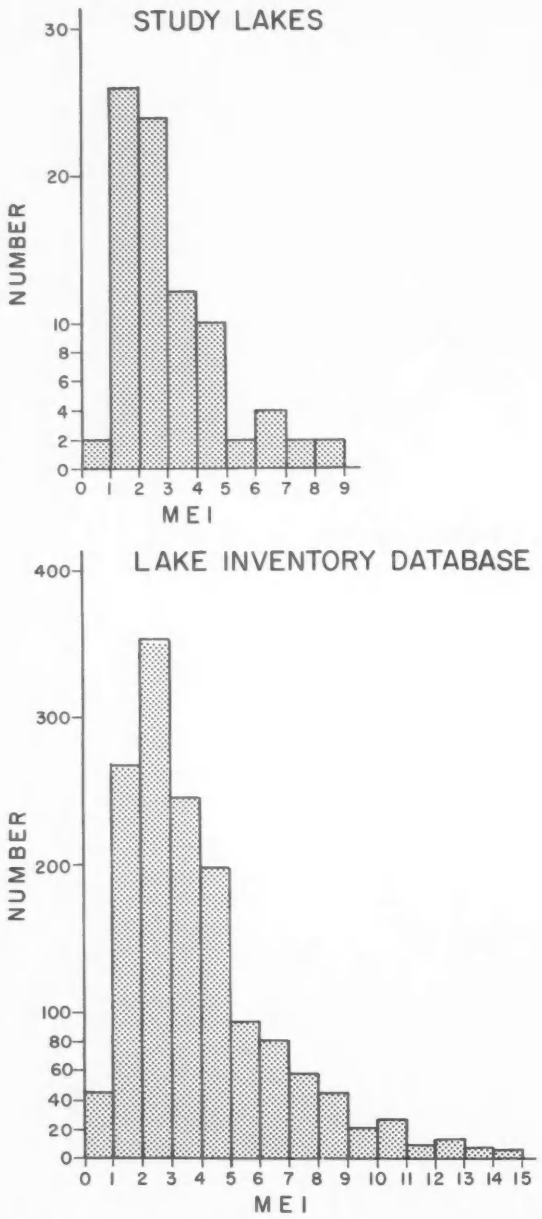

FIG. 1. Distribution of MEI values (TDS/$\bar{Z}$) for all the lake trout lakes in the Ontario Lake Inventory Database and the lake trout lakes selected for this study.

and to avoid any problems which could arise from historical shifts in the relationship between catch and effort (e.g. Shuter et al. 1987), lake trout annual catch and effort estimates from a single recent year were used to characterize each lake. For the lakes where estimates for several years were available, estimates for either 1980 or the year closest to 1980 were used. A complete list of the relevant data for all lakes, along with some summary statistics, is given in Table 1.

The extent to which the sample of lake trout lakes selected was representative of Ontario lake trout lakes in general was assessed by comparing the distribution of MEI values (TDS/$\bar{Z}$, Ryder 1965) in the sample with the MEI distribution for lake trout lakes in the OLIDB (Fig. 1). Values in the sample were negatively skewed, with essentially no representation above 9.0. Lake trout lakes with greater MEI values made up about 9% of the lake trout lakes in the OLIDB. Therefore, it was considered that the selected sample of 87 lakes provided a relatively accurate representation of typical lake trout fisheries, if not necessarily of lake trout lakes.

The primary objective was to examine the data set for evidence that differences in fish community structure affect lake trout catches in a consistent and predictable manner. The basic tool chosen to conduct the examination was analysis of covariance. A rationale for this choice is given below.

Consider the basic catch equation (Paloheimo and Dickie 1964)

$$(1)\quad \frac{C}{A} = \frac{E}{A} \cdot q \cdot \frac{N}{A}$$

where C is total catch, E is total effort, q is gear efficiency, N is population size, and A is the area occupied by the population. This implies that

$$(2)\quad C = E \cdot \frac{q}{A} \cdot N$$

and, if we assume that N is a simple function of A (i.e. $N \propto A^B$), then

$$(3)\quad C \propto a \cdot E \cdot A^d$$

or

$$(4)\quad \log_{10} C = a + b \log_{10} E + d \log_{10} A.$$

Equation 4 provided the basis for translating the overall objective into a specific plan of action. The data set was divided into groups of lakes that differed with respect to some aspect of fish community structure. Several different groupings were tried, using different aspects of community structure to define the groups. The groups were then compared by using analysis of covariance to determine if any of the coefficients in equation 4 differed systematically from group to group.

Groupings of lakes were based on differences associated with the following aspects of fish community structure: (a) The number of prey species for lake trout; yellow perch, lake herring, and rainbow smelt were identified as useable forage fish. For those lakes where lake trout was the only sport species present, the individual lake trout populations were identified as either planktivorous or piscivorous. (b) The number of potential competitors/associates with lake trout; burbot and lake whitefish were identified as potential lake trout competitors/associates.

In addition, the fish communities in the groups of lakes were defined in terms of the presence or absence of other fish species actively sought by anglers: brook trout; lake whitefish; smallmouth bass; walleye; and northern pike (OMNR 1978). Most of these species are not thought to be closely linked ecologically to lake trout, and therefore, any differences that might exist between groups defined according to these criteria could well be

TABLE 2. Groupings of lake trout lakes compared using analysis of covariance. Each grouping is classified by the general criterion used to define it: potential lake trout food resources; potential lake trout competitors/associates; availability of alternative sport fish. The number of lakes in each group is given in parentheses beside the group name. Individual species are referred to by the following codes: LT = lake trout; ST = rainbow smelt; LH = lake herring; YP = yellow perch; BB = burbot; LW = lake whitefish; BT = brook trout; SMB = smallmouth bass; W = walleye; NP = northern pike.

Food resources	Competitors/associates	Alternative sport fish
Lake trout only lakes with planktivorous LT (13) vs. lake trout only lakes with piscivorous LT (7)	Lakes with one of BB, LW (44) vs. lakes where BB and LW are both absent (35)	Four groups compared simultaneously; groups defined according to the number of angler target species (LT, LW, BT, SMB, W, NP)
Lakes with at least one of ST, LH, YP (60) vs. lakes where ST, LH, YP are all absent (19)	Lakes with BB (37) vs. lakes without BB (41)	Present: group 1-LT alone (20) group 2-LT + 1 target (28) group 3-LT + 2 targets (18) group 4-LT + 3 targets (11)
	Lakes with LW (39) vs. lakes without LW (47)	
Lakes with LH and YP (25) vs. lakes where ST, LH and YP are all absent (19)	Lakes with both BB and LW (26) vs. lakes where BB and LW are both absent (35)	Lakes with one of SMB, NP (45) vs. lakes where SMB, NP both absent (34)
Lakes with ST (7) vs. lakes without ST (70)		Lakes with one of BT, W (22) vs. lakes where BT, W both absent (57)
Lakes with LH (26) vs. lakes without LH (52)		Lakes with one of SMB, NP, BT (53) vs. lakes where SMB, NP, BT all absent (26)
Lakes with YP (56) vs. lakes without YP (22)		Lakes containing W (10) vs. lakes where W absent (69)

TABLE 3. Pearson correlation matrix for continuous variables in the data set. Each correlation coefficient is based on 87 observations. Values significant at the 5% level are marked with an asterisk. Variables are coded as follows: LTC = lake trout catch ($kg \cdot yr^{-1}$); EFF = angling-effort (angler-h$\cdot yr^{-1}$); AREA = lake area (ha); TDS = total dissolved solids ($mg \cdot L^{-1}$); $\bar{Z}$ = mean depth (m); MEI = TDS/$\bar{Z}$ ($N = 78$).

	LTC	EFF	AREA	TDS	$\bar{Z}$	MEI
LTC	1.0	0.860	0.850	0.049	0.275	−0.104
EFF	—	1.0	0.771*	0.041	0.335	−0.116
AREA	—	—	1.0	−0.087	0.193	−0.151
TDS	—	—	—	1.0	−0.054	0.837
$\bar{Z}$	—	—	—	—	1.0	−0.456*
MEI	—	—	—	—	—	1.0

TABLE 4. Results of stepwise multiple regression analysis of the dependence of lake trout catch (LTC) on fishing effort (EFF) and lake morphometry (AREA, TDS, $\bar{Z}$, MEI). Independent variables are listed in the order in which they were included in the stepwise procedure. All variables listed are statistically significant ($p = 0.05$, $N = 78$). The fraction of the variation in catch accounted for at each step (R^2) is also given.

	Dependent variable = $\log_{10}$ (LTC) Constant term (SE) = −1.172 (0.239)		
Independent variable	Coefficient (SE)	t-value	R^2
$\log_{10}$ (EFF)	0.595 (0.067)	8.94	0.729
$\log_{10}$ (AREA)	0.435 (0.075)	5.81	0.810

the product of interactions between angler preferences and the number and kind of sport fish available. The specific sets of groupings examined are listed in Table 2.

Results

Before proceeding with the covariance analyses outlined in Table 2, the complete data set was examined using correlation analysis and stepwise multiple regression. A Pearson correlation matrix for all continuous variables is given in Table 3. Stepwise multiple regression analysis (Table 4) of the dependence of lake trout catch on the effort and morphometric variables listed in Table 3 revealed that effort directed at lake trout and lake area each explained significant ($p < 0.01$) amounts of the overall variation in lake trout catch. The most important predictor by far was effort directed at lake trout, followed by lake area. The relatively high pairwise correlation between effort and area (Table 3) would tend to obscure the relative importance of these two variables in accounting for the variation in catch. It is possible that the relative importance of area is greater than that indicated by the change in the R^2 value noted in Table 4. The data and the regression equation are illustrated in Fig. 2.

The results of all the analyses listed in Table 2 can be summarized succinctly. Consistent, strong differences were not found within the three major categories listed in Table 2. One marginally significant difference was noted: lake trout catch in lakes with either brook trout or walleye was less than the catch in lakes where they were both absent ($p = 0.037$).

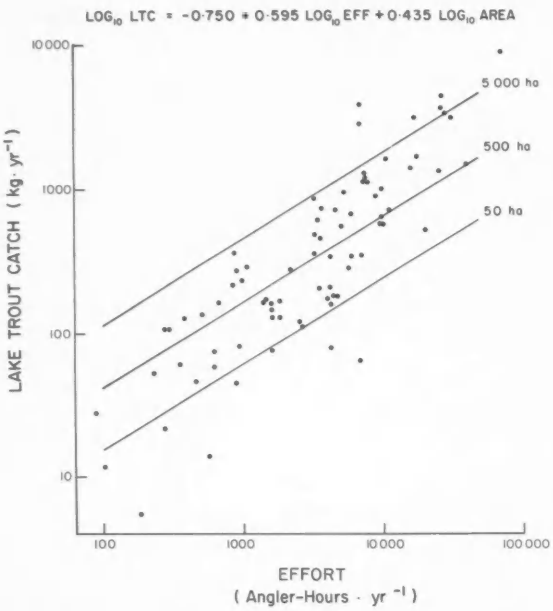

FIG. 2. Lake trout catch in relation to fishing effort. Regression lines calculated for lakes with areas of 50, 500, and 5000 ha.

Discussion

The MEI is the best single-point mathematical expression for estimating the potential yield of all fish species from lakes in Ontario. Nevertheless, effort appears to be the singlemost important factor in determining the actual yield of fish, actual yield being a function of potential yield and effort.

In the present study of lake trout lakes, effort directed at lake trout (angler-hours per year) explained 73% of the variation in actual catch of lake trout (kilograms per year) and was significantly correlated ($p < 0.05$) with lake trout catch in the Pearson correlation matrix (Table 3). The positive relationship between effort and catch was similar to the findings of Jenkins and Morais (1971) and Schlesinger and McCombie (1983).

The actual catch of lake trout was also correlated positively with lake surface area (hectares) and, together with effort, accounted for 81.5% of the variation (Table 4). It should be emphasized that lake trout catch and effort were not standardized by area in the present study, contrary to current practice (Youngs and Heimbuch 1982), thus eliminating the potential problem of having area as both a dependent and independent variable in the same equation. The positive relationship stands to reason, ceteris paribus, the larger the lake the more fish it can potentially produce.

Nevertheless, an inverse relationship between yield (catch-per-unit-area) and lake area was found (the coefficient for $\log_{10}$ area in Table 4 being significantly less than 1), which was consistent with reports by Rounsefell (1946), Carlander (1977), Oglesby (1977), and others. Our results are consistent, also, with this inverse relationship, the coefficient for log area in Table 4 being significantly less than 1. The inverse relationship implies, as noted by Ryder et al. (1974), that on a per unit area basis, smaller lakes are fished more efficiently and/or produce more fish than larger lakes.

A descriptive equation is offered that relates the actual catch of lake trout to the determining factors of angler-effort and lake surface area:

$$Y = 0.178(E^{0.595})(A^{0.435}).$$

In this equation ($R^2 = 0.81$), Y is the actual catch of lake trout (kilograms per year), E is the angler-effort (angler-hours per year), and A is the surface area (hectares).

Mean depth ($\bar{Z}$) was weakly correlated with the actual catch of lake trout in the pairwise comparison in the Pearson correlation matrix. Nevertheless, in a stepwise multiple regression, when the effects of effort and area were removed, $\bar{Z}$ was not significant, due to the strong correlation between $\bar{Z}$ and effort.

MEI, TDS, and mean depth were not useful predictors of the actual catch of lake trout in the present study. This was not unexpected, as the predictive power of these parameters was dependent to a large extent on the range of values within the data set. Mean $\bar{Z}$ was 14.9 ± 6.5 m and the range was 5.0–38.7 m (Table 2). Johnson et al. (1977) stated that lake depth distinguished lake trout lakes from other lakes with fair precision such that lakes with $\bar{Z} > 6$ m contained lake trout. The sample from the present study, therefore, was biased in favour of deep lakes. Similarily, the MEI and TDS values were low with very little variation (mean 3.2 ± 2.5 and 40.2 ± 24.3, respectively). As a consequence, the selection of only lake trout lakes and the inherent restricted $\bar{Z}$, TDS, and MEI values in the data set reduced their usefulness as predictors of the actual yield of lake trout.

On an a priori trophic–dynamic basis, one would predict that the type and presence–absence of the forage fish would affect the potential productivity of lake trout. In the present study, however, the presence–absence of rainbow smelt, lake herring, or yellow perch, either individually or in concert, did not affect the actual yield of lake trout. Moreover, the analyses could not detect a difference in actual yield between lakes where the lake trout fed primarily on zooplankton and lakes where the lake trout were piscivorous. If actual yield closely reflects potential productivity, then the finding is consistent with that of Martin (1966) and Kerr and Martin (1970) that the production of lake trout is not influenced by the differences in utilization of the food chain. Nevertheless, they noted that although overall production was the same, the growth rate and the nature of the fisheries were different: lakes with planktivorous lake trout produced high catches-per-unit-effort (CUE) and small fish whereas lakes with piscivorous lake trout produced relatively low CUE's, but larger fish. Similarly, Hanson and Leggett (1982) studied a wide variety of lakes with diverse fish communities and suggested that there was a nearly constant energy transfer from the benthos to fish, regardless of the number of fish species present. The present study, then, supports also the thesis that the yield of lake trout is independent of the nature of the food chain.

The actual yield of lake trout was not affected significantly by the associations with other fish species, either potential competitors/associates (burbot and lake whitefish) or alternative sport fish (brook trout, walleye, northern pike, smallmouth bass). Simply stated, fish community structure does not appear to affect the actual yield of lake trout. As a consequence, fish community structure cannot be used meaningfully as a predictor of actual lake trout yields.

It is possible, however, that yields may be weakly linked to

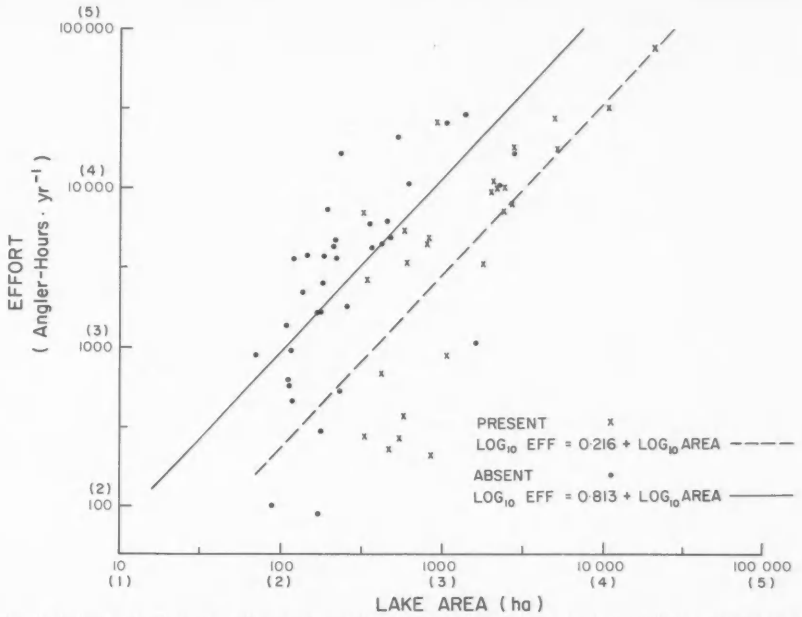

FIG. 3. Relationship between effort and area for lake trout lakes that contain both lake whitefish and burbot (×) and lakes which contain neither (●).

fish community structure, but that the linkages are too subtle to be distinguished with low-precision data from a relatively small number of lakes (i.e. the community contribution is masked by the overriding influence of area). Barbour and Brown (1974) found a strong relationship between number of species and surface area. Similarly, within the present data set, the number of sport fish species in the lakes was significantly correlated (Pearson's R, $p < 0.01$) to lake surface area in a Pearson correlation matrix. For example, the mean surface area of lakes containing only lake trout was 331 ha. By comparison, lakes containing lake trout, lake whitefish, and smallmouth bass had a mean surface area of 2966 ha whereas the mean surface area of lakes with lake trout, lake whitefish, smallmouth bass, walleye, and northern pike was 5520 ha.

Ecological theory suggests that changes in the basic production parameters of a fish population should result from changes in the number and character of the resource and competitor populations that interact with it. Findings of the present study seem to contradict this suggestion. That apparent contradiction, however, holds only if the actual yield is assumed to be closely and consistently related to potential production. Nevertheless, this assumption can be challenged. If angling-effort is responsive to past success or failure (i.e. high CUE in one year leads to an increase in effort in the next year; low CUE leads to a decrease), then observed *effort*, rather than the observed yield, will tend to correlate with the basic productivity of the population. More productive populations will be subject to higher levels of effort because, historically, they have proven capable of withstanding such levels, while still delivering CUE's which are acceptable to anglers. Evidence supporting this responsiveness was found in the present data set. For 32 of the 89 lakes, catch and effort values for two consecutive years were available; the change in effort from year 1 to year 2 was significantly ($p < 0.01$) and positively correlated with the CUE in year 1.

Consistent, strong differences were not detected when effort levels among the groupings listed in Table 2 (analysis of covariance on $\log_{10}$ effort, with $\log_{10}$ area as covariate) were compared. A significant difference, however, was detected between lakes with neither of the major competitor/associates and lakes which contained both. The effort on lakes with both burbot and lake whitefish was approximately 25% of the effort on lakes where they were both absent ($p < 0.001$, Fig. 3). This difference suggests that there may be a mixture of lower lake trout productivity and higher lake trout catchability in those lakes which contain both burbot and lake whitefish.

The results of the present study illustrate well the difficulties inherent in trying to draw inferences about the productivity of fish populations using catch and effort data alone. Depending on the nature of angler behaviour, differences in productivity will be reflected either by differences in yield or by differences in effort. If the response time of anglers to past success is relatively slow, or is quite erratic from lake to lake, then productivity differences will be largely obscured in both the catch and effort data, which could explain why consistent effects of community structure were not detected in the data set.

Management Implications

In Ontario lakes with self-sustaining fish populations, the potential fish production for all fish species is best predicted by using the physical and chemical factors intrinsic to the lake itself ($\bar{Z}$, TDS, MEI). The potential yield is then used as the guideline for estimating the allowable annual harvest. The actual harvest appears to be independent of the associated fish community structure.

Differences in the observed harvest of lake trout are largely associated with differences in angler-effort. The control of angler-effort, therefore, is essential if the annual harvest is to be

controlled. To control harvest effectively, however, managers require much more socio-economic data about angler preferences, responses to changes in CUE, and harvest control regulations. The significant correlations observed among catch, effort, and area may be simply that anglers fish a great deal when lake trout are abundant and not so much when CUE's for lake trout are low. The lakes used in the present study were fished moderately, as the mean relative yield intensity (RYI, the ratio of the estimated yield of all species to the potential yield; Adams and Olver 1977) was 0.56 (±0.44). The ratio of estimated yield of lake trout to the recommended yield of lake trout (25% of potential yield) was 1.63 ± 1.44. On average, 73% of the estimated total harvest was lake trout in the lakes containing alternative sport fish. This suggests that anglers target on lake trout and consequently tend to underharvest the other available sport fish in these lakes. Nevertheless, the emphasis on one fish species may effectively stimulate compensatory mechanisms with a resultant increase in recruitment and subsequently yield. The increased production of lake trout may be at the expense of other fish species, as suggested by Colby (1984).

A major problem in the present study was that the final sample size was numerically low. Although hundreds of creel surveys were checked, annual yields of lake trout could only be determined confidently for the 87 lakes. Also, many creel reports did not make any attempt to estimate the total yield of all species. Whenever possible, creel surveys should be designed to provide estimates of the total annual yield of all species and the associated effort and not just the yield of selected species.

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Colonization of Inland Lakes in the Great Lakes Region by Rainbow Smelt, *Osmerus mordax*: Their Freshwater Niche and Effects on Indigenous Fishes[1]

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Evans, D. O., and D. H. Loftus. 1987. Colonization of inland lakes in the Great Lakes region by rainbow smelt, *Osmerus mordax*: their freshwater niche and effects on indigenous fishes. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 249–266.

Rainbow smelt, *Osmerus mordax*, have colonized numerous inland lakes in eastern North America, primarily as a result of introductions by humans. Smelt often establish large populations in these lakes and influence indigenous fishes both directly (predation) and indirectly (competition). Smelt have a eurythermal life history, which results in spatial segregation of their larvae, juvenile, and adults, and are omnivorous feeders, eating a range of food types from zooplankton to fish. As a result, smelt interact strongly with a wide spectrum of prey and predator species. Effects on other species are mediated via food web interactions resulting in recruitment and growth changes in some species and redirection of energy flow and storage. Species most often affected are cold-water and cool-water species whose niches are most similar to juvenile and adult smelt. Increased growth rates of Atlantic salmon (*Salmo salar*) and lake trout (*Salvelinus namaycush*) and recruitment failure of lake whitefish (*Coregonus clupeaformis*) are the best documented responses to invasion by smelt. Many other species are probably also affected, although the effects vary greatly between lakes. Variation in the smelt metabolic niche (as expressed by relative growth efficiency) is due to variations in prey size and availability and is reflected in differences in smelt body size between lakes. Smelt body size, in turn, is related to the variable effects that they have on other species.

L'éperlan arc-en-ciel, *Osmerus mordax*, a colonisé, surtout suite à son introduction par l'homme, un très grand nombre de lacs intérieurs de l'est de l'Amérique du Nord. Les populations d'éperlan ont souvent été importantes et ont influé sur les poissons indigènes de façon directe (prédation) et indirecte (compétition). L'éperlan a un cycle vital eurytherme, ce qui se traduit par une ségrégation spatiale des larves, des juvéniles et des adultes, et est omnivore, se nourrissant d'une large gamme de proies qui vont du zooplancton aux poissons. Tout ceci est à l'origine de fortes interactions avec une large gamme d'espèces proies et prédatrices. Les effects sur les autres espèces se produisent par l'intermédiaire d'interactions au sein du réseau alimentaire qui résultent en des modifications du recrutement et de la croissance de certaines espèces et en une réorientation des flux énergétiques et du stockage. Les espèces les plus souvent affectées sont les espèces d'eaux froides et fraîches dont les niches s'apparentent le plus à celles des éperlans juvéniles et adultes. On compte, parmi les effets les mieux connus de l'invasion par l'éperlan, l'accroissement des taux de croissance du saumon de l'Atlantique (*Salmo salar*) et du touladi (*Salvelinus namaycush*) et l'échec du recrutement chez le corégone de lac (*Coregonus clupeaformis*). Bon nombre d'autres espèces sont probablement affectées, mais les effets varient fortement d'un lac à l'autre. La variation de la niche métabolique de l'éperlan (exprimée par l'efficacité relative de la croissance) découle de variations de la taille et de la disponibilité des proies et se traduit par des écarts de la taille des éperlans entre les lacs. La taille des éperlans est à son tour fonction des effets variables de cette espèce sur les autres espèces.

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Rainbow smelt, *Osmerus mordax*, is an indigenous species of glaciomarine origin in many freshwater lakes of eastern North America (Kendall 1926; Dadswell 1974). In the region of the Great Lakes, however, this species has been widely introduced, beginning with an intentional and successful introduction to Crystal Lake, Michigan, in 1912 (Creaser 1925). Subsequent expansion of range in the Great Lakes is well documented (Van Oosten 1947; Dymond 1944; Christie 1974; Bergstedt 1983). Rainbow smelt have rapidly expanded their range in Ontario in recent years, having first appeared in three of the largest lakes, Simcoe, Nipissing, and Nipigon, in 1961, 1964, and 1976, respectively (Borecky et al. 1982; MacCrimmon et al. 1983a; K. Jorgenson, Ontario

[1]Contribution No. 86-15 of the Ontario Ministry of Natural Resources Research Section, Fisheries Branch, Box 50, Maple, Ont. L0J 1E0.

Ministry of Natural Resources (OMNR), North Bay, pers. comm.). Numerous small lakes have also been invaded during this period, raising concern about the possible effects on several important sport and commercial species, including lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), lake herring (*Coregonus artedii*), and walleye (*Stizostedion vitreum vitreum*). Speculation about the effects of rainbow smelt on fish communities in the Laurentian Great Lakes (Smith 1968; Christie 1972; Christie et al. 1972; Smith 1972; Regier 1973) and in smaller inland lakes (Loch et al. 1979; Hassinger and Close 1984) has prompted this concern.

Rainbow smelt affect other fishes directly by predation on their young (O'Gorman 1974; Foltz and Norden 1977; Selgeby et al. 1978; Stedman and Argyle 1985; Loftus and Hulsman 1986), but also indirectly by changing food web structures and routes of energy flow in aquatic systems. Smelt redirect energy flow by serving as an alternate or primary prey (Eck and Brown 1985) and as a competitor of indigenous species (Crowder et al. 1981) or both. Christie (1974) speculated that replacement of indigenous planktivores (deepwater ciscoes and lake herring) in Lake Ontario by rainbow smelt and alewife (*Alosa pseudoharengus*) has resulted in a loss of verticle vectoring of energy from the abyss of the lake. The efficiency of nutrient cycling in lakes dominated by smelt is, therefore, also in question, as is the influence of shifting patterns of energy flow on size-linked species interactions and ultimately on community structure.

The aim of this study is to identify the types of lakes and fish communities that have been successfully colonized by rainbow smelt, to document the apparent effects of rainbow smelt on other fish species, and to describe the trophic and spatial relationships between rainbow smelt and other species in freshwaters. The size spectrum of the smelt diet in relation to relative growth efficiency (Kerr and Ryder 1977) and distributional life history is compared in freshwater and marine habitats to evaluate the phenotypic plasticity of the rainbow smelt niche and the species' corresponding roles in vectoring of energy in lakes. Kerr and Ryder (1977) described the metabolic niche of percid species in Lake Erie using growth efficiency (K) as a niche separator. Different K-lines indicated different realized niches within the same habitat. We take growth efficiency patterns to be a reflection of species interactions associated with prey resource utilization and therefore of the ecological role of a species in a given habitat.

We employ a large data base for lakes in Ontario, Canada, to describe the types of lakes and fish communities invaded by rainbow smelt and compare case studies of rainbow smelt introductions throughout eastern North America for evidence of effects on other species. New information on diet and growth efficiency is reported and data on distribution, diet, and species interactions are summarized from the published literature.

Methods

Data on the distribution of rainbow smelt in Ontario have been obtained through computer searches of the Lake Inventory Data Base (LIDB), Ontario Ministry of Natural Resources (OMNR), which at the present time contains information on limnological characteristics and fish species for 8842 Ontario lakes; the Fish Species Distribution Data Base, based on records of the National Museums of Canada and Royal Ontario Museum; and through a questionnaire sent to each of 47 OMNR field offices located throughout Ontario. Two data sets were generated: one consists of a list of all lakes known to contain rainbow smelt, their latitude, longitude, OMNR administrative Region and District, watershed, date, and source of introduction, and the type of information documenting the presence of smelt; the second data set contains selected limnological characteristics of these same lakes and the fish species present. Information was also compiled on the status of the existing fish community prior to and after the introduction of rainbow smelt.

Stomach analyses were performed on 225 rainbow smelt captured by gill nets in Lake Huron during August and September 1984 to determine the relationships between smelt body size and their degree of piscivory and maximum prey size.

Results

Distribution of Rainbow Smelt in Ontario

Rainbow smelt are known to occur in 194 inland lakes in Ontario, although 7 of these are tentative designations based on unconfirmed reports (Fig. 1). This species is also found in all five Laurentian Great Lakes. Indigenous populations occurred in four inland lakes in eastern Ontario (Muskrat, Dore, Golden, and possibly Timiskaming) as a result of inundation by the Champlain Sea, ca. 11 000 yr B.P. (Radforth 1944). The origin of smelt in Lake Timiskaming (elevation 178 m) is unknown, but Dymond (1937) noted that the Champlain Sea extended to the head of Lake Timiskaming. Coleman (1941, p. 94) also noted this possibility. The Champlain Sea did reach 210 m above sea level near Ottawa (Coleman 1941; see also Prest 1976), 38 m above present-day Lake Timiskaming, and four species of invertebrates of "glaciomarine origin" occur in Lake Timiskaming (Dadswell 1974), supporting the contention that rainbow smelt is an indigenous resident. Most Ontario lakes containing smelt lie within the drainage basins of the Great Lakes and St. Lawrence River, with the exception of several lakes near Quetico Park which are within the Arctic watershed.

Introduction by humans appears to be the primary means of invasion and colonization. This is indicated by the strong association of lakes containing rainbow smelt with urban and cottage development. In all cases, introductions have been unofficial and, in many cases, probably unintentional. The majority of these introductions have probably resulted from inadvertent fertilization and release of eggs into the new environment during processing (cleaning) of sexually mature smelt captured elsewhere during spring spawning runs. Intentional introduction, through the release of adult smelt or by transporting and releasing fertilized eggs (Richardson and Belknap 1934), has also undoubtedly occurred in some instances.

The secondary mechanism of colonization is movement through interconnected waterways (Kriksunov and Shatunovsky 1979). In Ontario, for example, smelt were recorded in St. Nora Lake near the headwaters of the Gull River in the 1950s and subsequently have become established in 13 downstream lakes in the Gull River chain spanning a distance of approximately 40 km. Similar movement has occurred in the Rainy River watershed in northwestern Ontario and is suspected in others.

Lakes colonized by rainbow smelt range in size from a few hectares to tens of thousands of square kilometres (the Great Lakes). In general, they are moderately deep lakes with average mean and maximum depths of 11.6 and 35.7 m, respectively, and range from slightly acidic to alkaline, having medium transparency and low productivity (Table 1). The number of fish

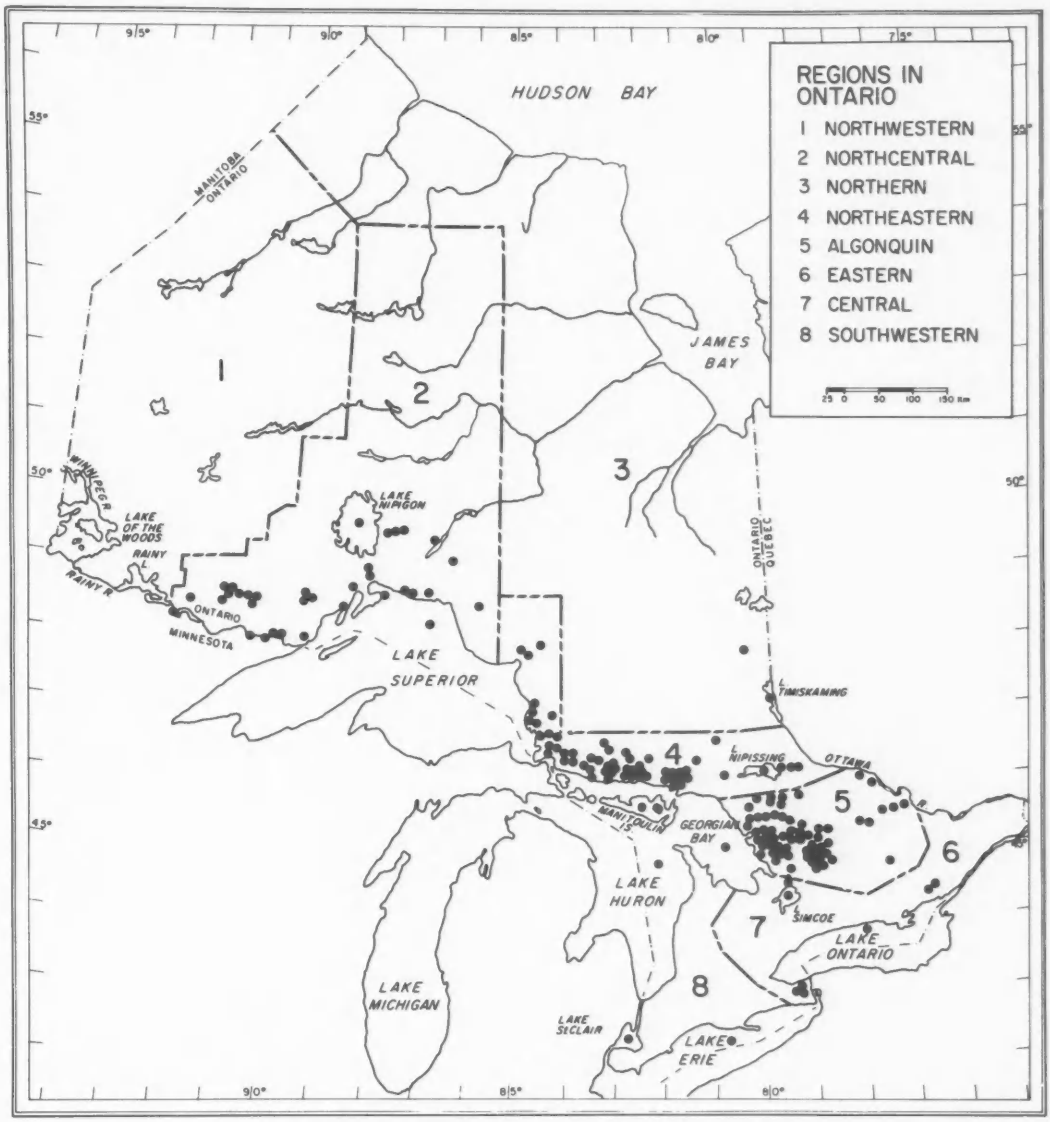

FIG. 1. Distribution of lakes in Ontario inhabited by rainbow smelt.

species present in Ontario lakes successfully invaded by rainbow smelt populations varied from 2 to 62 in inland waters and from 67 to 114 in the Great Lakes (Ryder 1972) prior to invasion by smelt. Species number in these lakes varies directly in proportion to lake size (Table 2).

Surface area explains 41.9% of the total variability in species number in inland lakes inhabited by rainbow smelt, and elevation alone explains 5.7%; when combined, these variables explain 43.5% of the variation (Table 2, equations 1–3). When the Great Lakes are included in the analysis, surface area and elevation explain 63.6 and 16.1%, respectively, of the total variation in species number, and the species–area coefficient increases from 0.164 to 0.199. Again, area alone accounts for most of the variation, elevation accounting for about 1.2% of the total variation when both variables are combined (Table 2, equations 4–6). Other variables that are correlated with species number are lake perimeter, shoreline development factor, mean and maximum depth, total dissolved solids, and alkalinity, but all have negligible effects when combined with surface area and elevation. Neither transparency nor morphoedaphic index (MEI, Ryder 1965) is significantly correlated with species number in these lakes.

Species Associations in Ontario Lakes Invaded by Rainbow Smelt

The frequency of occurrence of 36 fish species is compared for 187 lakes containing rainbow smelt and all 8842 lakes (both

TABLE 1. Summary of morphometric, limnological, and fish species information for 187 lakes reported to have populations of rainbow smelt. The data are not complete for all lakes. Alkalinity is determined as total fixed endpoint.

Parameter	Number of lakes	Mean	Minimum	Maximum	Median	Lower quartile	Upper quartile
Elevation (m)	173	278.1	123.0	457.0	270.0	221.0	328.0
Area (km^2)	177	52.3	0.1	4,480.0	3.0	1.2	9.6
Perimeter (km)	173	38.4	1.4	933.2	14.2	8.0	34.8
Volume (10^6 m^3)	168	35.2	0.4	1,230.0	3.0	0.9	10.7
Mean depth (m)	169	11.6	2.0	38.7	9.5	6.8	14.9
Maximum depth (m)	181	35.7	4.0	213.5	27.5	19.5	43.0
Total dissolved solids (mg/L)	135	49.4	5.5	231.4	36.0	27.0	57.9
Alkalinity (mg/L)	170	25.0	4.0	145.4	17.1	12.0	27.3
Surface pH (May–Aug.)	173	7.2	6.0	9.3	7.0	6.8	7.5
Hypolimnion pH	158	6.5	5.5	9.0	6.4	6.0	6.8
Secchi (m)	172	4.9	1.3	10.5	5.0	3.6	5.9
MEI (TDS/mean depth)	128	5.9	0.6	45.3	3.7	2.2	7.6
Number of fish species[a]	179	11.3	3.0	63.0	10.0	8.0	12.0

[a]Census of the Family Cyprinidae may not be complete.

TABLE 2. Linear regression values and statistical significance for number of species versus lake surface area and elevation in Ontario lakes inhabited by rainbow smelt.

No.	Variables (Dependent × independent)	n	$y = a + bx$ a	b	S_b	b/S_b	p	R^2(%)
	Inland Ontario lakes							
1	log no. spp. × log area (km^2)	177	0.91	0.164	0.015	11.2	≤0.01	41.9
2	log no. spp. × log elevation (m)	172	2.03	−0.419	0.131	−3.2	≤0.01	5.7
3	log no. spp. × log area	170	1.39	0.159	0.015	10.6	≤0.01	42.3
	× log elevation			−0.194	0.104	−1.9	≤0.05	1.2
	Inland Ontario lakes and the Great lakes combined							
4	log no. spp. × log area	182	0.89	0.199	0.011	17.1	<0.01	63.6
5	log no. spp. × log elevation	177	3.09	−0.847	0.146	−5.8	<0.01	16.1
6	log no. spp. × log area	175	1.54	0.188	0.012	15.7	<0.01	64.0
	× log elevation			−0.262	0.102	−2.6	<0.01	1.3

with and without smelt) in the LIDB (Table 3). White sucker (*Catastomus commersoni*), smallmouth bass (*Micropterus dolomieui*), and yellow perch (*Perca flavescens*) are found in 70% or more of the lakes inhabited by rainbow smelt. These species are found more frequently in smelt lakes than in Ontario lakes in general, especially smallmouth bass which are four times more common in smelt lakes than in other Ontario lakes. A strong positive association is also found between smelt and lake trout (percent difference +33.9), lake whitefish (percent difference +35.8), and lake herring (percent difference +23.8) (Table 3), species that are usually found in deep, cold lakes. Rock bass (*Ambloplites rupestris*), pumpkinseed (*Lepomis gibbosus*), brown bullhead (*Ictalurus nebulosus*), and burbot (*Lota lota*) are also strongly associated with rainbow smelt (percent differences >19.5). Of these species, white sucker, yellow perch, lake whitefish, lake herring, burbot, and brown bullhead are probably indigenous to most of the lakes they cohabit with smelt. Many of the other species associated with rainbow smelt have been widely introduced, especially in the Algonquin and Northeastern regions of Ontario (Fig. 1) where rainbow smelt are most common. This suggests the common influence of human activity in determining the patterns of distribution for several species, especially those associated with angling, including species that have been extensively stocked (lake trout, smallmouth bass) and others that are used as bait (Cyprinidae, Percidae) or are transported inadvertently with bait by anglers.

Case Studies of Rainbow Smelt Introductions

Of the case studies that we have recorded (Table 4), 13 of 24 involve recruitment declines of lake whitefish (the Fish River lakes (Warner and Fenderson 1963) are counted as a single case, but comprise eight lakes, seven of which have had introductions of rainbow smelt; lake whitefish subsequently disappeared from these lakes; Fish Lake, which is the headwater lake in the chain, has been colonized by smelt only relatively recently and is now experiencing recruitment failure of lake whitefish (K. Warner, Maine Department of Inland Fish and Wildlife, Bangor, ME)), and 5 of 19 report declines in lake herring. In eight others (Champlain, Crystal (Michigan), Gull (Michigan), Owasco, Sebago, Golden, Timiskaming, and Skootamatta), either lake whitefish or lake herring, or both, appear to be relatively successful in the presence of rainbow smelt. Whitefish and lake herring are absent in the two Ontario lakes with large indigenous smelt populations (Dore and Muskrat), and indigenous smelt are rare or have disappeared from two lakes that continue to support

TABLE 3. Comparison of the frequency of occurrence of selected fish species in 187 inland lakes in Ontario with rainbow smelt populations and in all 8842 surveyed lakes with and without smelt.

Species name	Status (n = native, i = introduced, e = exotic, b = bait)	187 smelt lakes		8842 survey lakes		
		No. of lakes	% of total	No. of lakes	% of total	% difference
Common white sucker	n	106	88.3	5960	67.4	+20.9
Smallmouth bass	n–i	88	73.3	1605	18.2	+55.1
Yellow perch	n	84	70.0	5266	59.6	+10.4
Lake whitefish	n	68	56.6	1837	20.8	+35.8
Lake herring	n	66	55.0	1878	21.2	+23.8
Lake trout	n–i	63	52.5	1646	18.6	+33.9
Rock bass	n–i	57	47.5	1293	14.6	+32.9
Pumpkinseed	n–i	56	46.7	1848	20.9	+25.8
Brown bullhead	n	49	40.8	1153	13.0	+27.8
Northern pike	n	45	37.5	3880	43.9	−4.4
Burbot	n	41	34.2	1281	14.5	+19.7
Bluntnose minnow	n–b	34	28.3	999	11.3	+17.0
Spottail shiner	n–b	32	26.7	1472	16.6	+10.1
Walleye	n–i	27	22.5	2345	26.5	−4.0
Longnose sucker	n	24	20.0	464	5.3	+14.7
Largemouth bass	n–i	24	20.0	724	8.2	+11.8
Creek chub	n–b	22	18.3	834	9.4	+8.9
Rainbow trout	e	19	15.8	269	3.0	+12.8
Brook trout	n–i	19	15.8	1767	20.0	−4.2
Golden shiner	n–b	17	14.2	1066	12.6	+1.6
Common shiner	n–b	15	12.5	981	11.1	+1.4
Iowa darter	n	15	12.5	1484	16.8	−4.3
Blacknose shiner	n–b	12	10.0	1549	17.5	−7.5
Brook stickleback	n	12	10.0	405	4.5	+5.5
Trout perch	n	12	10.0	415	4.7	+5.3
Log perch	n	12	10.0	536	6.1	+3.9
Pearl dace	n	11	9.2	894	10.1	−0.9
Northern redbelly dace	n–b	9	7.5	1563	17.7	−10.2
Lake chub	n–b	9	7.5	506	5.7	+1.8
Johnny darter	n	8	6.7	1014	11.4	−4.7
Fathead minnow	n–b	7	5.8	1196	13.5	−7.7
Emerald shiner	n–b	6	5.0	219	2.5	+2.5
Muskellunge	n–i	5	4.1	178	2.0	+2.1
Bluegill	n	5	4.1	238	2.7	+1.4
Alewife	e	4	3.3	29	0.3	+3.0

coregonines (Golden Lake and Lake Timiskaming). Other observations associated with smelt invasions include increased growth rates or change in condition of lake trout and Atlantic salmon (*Salmo salar*) (10 cases), decreased growth or recruitment of juvenile lake trout (7 cases), recruitment failure of walleye (3 cases) and burbot (1 case), and competition with or displacement of smelt by alewife (2 cases). Because of the correlative and often qualitative nature of these observations, however, none of the species responses in these case studies can be definitively attributed exclusively to the effects of rainbow smelt. Nevertheless, the evidence is relatively convincing in the cases of lake whitefish recruitment failure and growth rate changes of lake trout and Atlantic salmon.

Spatial and Trophic Niche Characteristics

In lakes, rainbow smelt have a eurythermal life history. They partition the nearshore zone from 0 to 60 m into three strata spanning warm- (young-of-the-year), cool- (yearlings), and cold-water (adults) habitats (Table 5). Adults in large lakes occupy the hypolimnion during the summer period of thermal stratification. They display a diel behaviour pattern, however, involving dispersal from the lake bottom into the water column at night, often ascending through the thermocline into the epilimnion (Ferguson 1965; Heist and Swenson 1983). Age 0 smelt, in Lake Michigan, appear to undergo an opposite diel movement from the epilimnion to the hypolimnion (Brandt et al. 1980). Yearlings are found in an intermediate position between the young and adult fish. This behavior enables smelt to utilize the spatial, thermal, and food resources of the lake bottom and entire water column, while minimizing intraspecific interactions.

Although rainbow smelt have a reputation for being "voracious" (Schneider and Leach 1977), their diet is dominated by such invertebrates as copepods, cladocerans, mysids, and insects (Table 6; Fig. 2). In cases such as Gull Lake (Burbidge 1969), Lake Erie (Ferguson 1965), and Lake Simcoe (MacCrimmon and Pugsley 1979), the extent of piscivory in smelt is quite low. Smelt are, nonetheless, capable of feeding on items as large as 6% of their body weight (Fig. 3), and given the opportunity will do so. Also, in some lakes and during certain seasons, large smelt may be almost wholly piscivorous. In Lake

TABLE 4. Summary of case history studies of the introduction of rainbow smelt and the subsequent status of Atlantic salmon (AS), lake trout (LT), lake whitefish (LW), lake herring (LH), and other species. Status codes: A = absent, P = present (no change), G = growth enhancement, R = recruitment decline, × = no noticeable change. Observations are often qualitative and do not necessarily indicate direct causal relationships with rainbow smelt. In Canadaiqua Lake, alewife recruitment increased and smelt declined.

Lake	Location	Area (ha)	Mean depth (m)	Smelt population status	Status of cold-water fish species						Reference(s)
					AS	LT	LW	LH	Other	No change	
Big Basswood Lake	Ontario	2 707	38.7	Introduced	A	G	G	A			P. Purych, OMNR, Sault Ste. Marie, pers. comm.
Canadaiqua Lake	New York	—	—	Introduced	A	P	P	R	Alewife (R)		Eaton and Kardos 1972; Kircheis and Stanley 1981
Cayuga Lake	New York	17 200	54.5	Introduced	A	P	R	R			Youngs and Oglesby 1972
Chiblow Lake	Ontario	316	23.9	Introduced	A	P	R	P			P. Purych, OMNR, Sault Ste. Marie, pers. comm.
Crystal Lake	Michigan	3 930	20	Introduced	A	P	P	P		×	Laarman 1976
Crystal Lake	Ontario	613	15.4	Introduced	A	R, G	P	R	-		Maher 1983
Dore Lake	Ontario	1 468	7.6	Indigenous	A	A	A	A		×	K. Buckingham, OMNR, Pembroke, pers. comm.
Devilfish Lake	Minnesota	161	4	Introduced	A	P	A	A		×	Hassinger and Close 1984
Echo Lake	Maine	96	—	Indigenous	A	A	P	A	Alewife (G)		Kircheis and Stanley 1981; Lackey 1969
Elliot Lake	Ontario	616	15.6	Introduced	A	G, R	R	P	Burbot (R)		Gray and Maraldo 1982; Maraldo et al. 1985 Maher 1983
Eva Lake	Ontario	1 709	13.5	Introduced	A	G	P	R			
Fish River lakes	Maine	8 lakes		Introduced	G	R	R	?			Warner and Fenderson 1963; K. Warner, Maine Dep. Inland Fish Wildl., Bangor, pers. comm.
Golden Lake	Ontario	3 552	8.5	Indigenous	A	A	P	?		×	Radforth 1944
Gull Lake	Ontario	996	16.5		A	P	R	P			W. Wilson, OMNR, Minden, pers. comm.
Gull Lake	Michigan	820	—	Introduced	A	P	A	P			Burbidge 1969
Lac Heney	Quebec	1 244	18.3		?	P	R	P			Legault and Delisle 1968
Lake Champlain	New York Vermont	—	—	Indigenous	P	P	P	P		×	Kendall 1927; Van Oosten and Deason 1938
Lake Simcoe	Ontario	72 500	17.0	Introduced	A	R	R	P			Evans 1978; Evans and Waring 1987
Lake Timiskiming	Ontario Quebec	29 507	35.7	Indigenous	A	P	P	P		×	K. Koski, OMNR, Temagami, pers. comm.
Loughborough Lake	Ontario	739	7.4	Introduced	A	R	R	R			Von Rosen 1970; Kunkle and Palilionis 1982
Love Lake	Maine	672	5.2	Introduced	G	?	?	?			Havey 1974
Manitou Lake	Ontario	10 461	15.1	Introduced	A	P	R	P			J. Reckahn, OMNR, South Baymouth, Manitoulin Island, pers. comm.
Moosehead Lake	Maine	30 307	—	Introduced	P	P	R	A			AuClaire 1978; Warner, Maine Dep. Fish., pers. comm.
Muskrat Lake	Ontario	1 244	17.7	Indigenous	A	A	A	A		×	Dymond 1937
Owasco Lake	New York	—	—	Introduced	A	?	?	P			Youngs and Oglesby 1972

TABLE 4. (*Concluded*)

Lake	Location	Area (ha)	Mean depth (m)	Smelt population status	Status of cold-water fish species						Reference(s)
					AS	LT	LW	LH	Other	No change	
Quabbin Reservoir	Massachusetts	10 125	15.2	Introduced	G	G	A	A			Bridges and Hambly 1971
Schoodic Lake	Maine	157	6.7	Introduced	G	A	A	A			Harvey 1973
Sebago Lake	Maine	11 643	31.6	Indigenous	P	?	P	?		×	Kendall 1927; Fenderson 1964
South Bay, Lake Huron	Ontario	7 490	20.2	Introduced	A	R	R	P			Henderson and Fry 1987
Sporley Lake	Michigan	96	—	Introduced	A	A	A	A	Zooplankton (R)		Galbraith 1967
Twelve Mile Lake	Ontario	715	23.1	Introduced	A	P	R	P			Loftus and Hulsman 1986
West Bearskin Lake	Minnesota	200	21.3	Introduced	A	G	A	A		×	Hassinger and Close 1984
Skootamatta Lake	Ontario			Introduced	A	R	P	P	Walleye (R)		D. Gibbs, K. Coleman, OMNR, Tweed, pers. comm.
Lucerne Lake	Wisconsin	415	7.4	Introduced	A	A	R	?	Walleye (R)		Colby et al. 1987
Fence Lake	Wisconsin	1 352	8.7	Introduced	A	A	A	A	Walleye (R)		Colby et al. 1987

Ontario, for example, fish comprised more than 45% of the dry weight of food of smelt between 150 and 200 mm between July and December and from 55 to 100% of the food of larger smelt; fish also comprised at least 79% of the food of all smelt longer than 100 mm during the summer months in Matamek Lake, Quebec (Chen 1970). Stomach analyses of rainbow smelt from Lake Huron revealed a similar increase in piscivory with body size (Fig. 4).

Rainbow smelt feed on a wide variety of fish species, including the young of large species such as lake trout, lake whitefish, and burbot. Extensive predation on young bloater (*Coregonus hoyi*), lake whitefish, lake herring, and alewife and on adult emerald shiner (*Notropis atherinoides*), has been observed in some instances (Beckman 1942; O'Gorman 1974; Stedman and Argyle 1985; Loftus and Hulsman 1986). With few exceptions, however, a high degree of piscivory in freshwater smelt reflects a high degree of cannibalism. In Lake Heney (Delisle 1969) and Matamek Lake (Chen 1970), where alternate fish prey occur at low densities, growth of piscivorous smelt may be sustained entirely by cannibalism, although in the former it is not cannibalism but predation on pygmy smelt (*Osmerus spectrum*) (Lanteigne and McAllister 1983) by the larger rainbow smelt.

In its native, marine environment, the smelt is an anadromous fish that spawns in freshwater and remains in estuarine and coastal areas at other times (McKenzie 1964; Leim and Scott 1966; Flagg 1972; Murawski and Cole 1978). Available information on the distribution of marine smelt (Rogers 1939; Murawski et al. 1980; McKenzie 1964; Ouellet and Dodson 1985a, 1985b) indicates that tidal influences and larger geographic scale result in greater spatial separation of age groups. This appears to correspond with lower levels of cannibalism in the marine environment. The marine smelt feeds on zooplankton, amphipods, shrimp, nereid worms, and small fish such as herring, mummichogs, and silversides (Marcotte and Tremblay 1948; Belyanina 1969), indicating a preference for relatively large prey. Cannibalism among marine smelt is possibly less prevalent because of greater spatial segregation of smelt size classes or because prey in marine waters tends to be more abundant and of larger size. In small inland lakes, the habitat is much more confined and less dynamic, presenting a greater opportunity for cannibalism to occur, which it does. The preference for relatively large food particles in marine waters and the high incidence of cannibalism in freshwaters indicate the propensity of smelt to eat relatively large prey. This further suggests an opportunistic strategy in freshwater in which large prey would be eaten whenever available in good supply and that the effects of smelt on indigenous fishes might, in part, depend on the availability of alternate prey.

Growth Efficiency, Body Size, and Diet

Growth efficiencies of selected smelt populations, for which size at age data are available, revealed that the metabolic niche of smelt in freshwater is highly variable (Fig. 5). The five growth efficiency curves (*K*-lines) shown span the range of growth patterns known for smelt in fresh and marine waters (Table 7). Comparison of smelt diet items versus smelt body size (Fig. 2) indicates four major diet transition points: one at 0.5 g marks the transition between small zooplankton and larger zooplankton and small mobile invertebrates (mysids and amphipods), the second at 2 g marks the transition to larger invertebrates, the third at about 10–20 g marks the initial occurrence of piscivory and cannibalism, and the fourth at about 50 g indicates initial predation on adult smelt. Comparison with Fig. 5 suggests that Lake Heney dwarf smelt, which do not exceed a body weight of 10 g, are primarily planktivores, that Lake Simcoe and Lake Superior smelt are occasional piscivores, but primarily benthivores, and that smelt in Lake Ontario and Muskrat Lake prey primarily on large invertebrates and fish. The range of *K*-lines depicted in Fig. 5 appears to describe the full phenotypic range of the metabolic niche of rainbow smelt and to reflect the ecological potential of the species in freshwater.

TABLE 5. Information on depth and temperature distribution of rainbow smelt. The temperature mode refers to the most frequently occupied temperature or region of the thermal distribution. In some cases, temperatures were calculated by the original authors, and in others, ranges were estimated from graphs or tables.

Lake	Sampling gear (depth sampled)	Life stage	Time of sampling	Distribution of rainbow smelt: Depth (m) Range	Depth (m) Maximum abundance	Temperature (°C) Range	Temperature (°C) Mode	Reference
Lake Erie (Wheatley to Port Dover)	Midwater trawl (6–46 m)	YOY	Aug.	6–15	Epilimnion	>21	>21	Ferguson 1965
			Oct.	3–40	4–5			
		Yearling	July	3–10	4–5	>15	>15	
			Oct.	10–23	18	>15	>15	
		Adult	Aug. (day)	20–46	24–46	6–10	6–7	
		Adult	Aug. (night)	18–46	20–46	6–>15	6–15	
Long Point Bay	Midwater trawl (0–40 m)	Yearling	Early May	21–38	38	—	—	Ferguson 1966
			Late May	3–10	—	7–10	—	
			Late June	—	—	10–15	—	
			July			<15	—	
			Early Aug.	24		—	—	
			Mid-Aug.	—		7–10	—	
			Sept.	35		—	—	
			Oct.	—		7–10	—	
Central and eastern basins	Midwater trawl (0–46 m)	YOY	June	<15		—	18	MacCallum and Regier 1970
			Mid-Aug.	—	10	—	—	
		Yearling	Midsummer	<18		12–18	—	
		Adults	Late Aug.	>18		—	—	
			Early summer	>18		—	—	
			Late summer	>18		—	—	
Lake Huron, Saginaw Bay	Bottom trawl (2–30 m)	YOY	July–Sept.	6–13	—	—	—	Carr 1962
			Oct.	6–18	18	—	—	
		Adult	Aug.	6–32	32	<15	—	
Lake Huron, South Bay	Otter trawl (4–58 m)	Adult	Aug.–Sept.	—	42–50	6.2–18.9	7.0	Reckahn 1970
Lake Superior, Apostle Islands	Otter trawl (3–27 m)	YOY and yearling	Apr. – July	<18–71	<18	--	>15	Dryer 1966
			July – Sept. 15	<18–35	<18	—	>15	
			Sept. 16–Dec. 13	<18–71	<18	—	—	
		Adults	Apr. – July	18–71	46	—	—	
			July – Sept. 15	18–71	36	—	<15	
			Sept. 16–Dec. 13	18–71	27	—	—	
Lake Superior (western arm)	Midwater trawl echo sounder (2–50 m)	All life stages	June – Aug.					Heist and Swenson 1983
			Day	2–40	25–30	—	6	
			Night	2–40	10–15	6–18	11–16	
			All times	<100	<50	—	—	
Lake Michigan	Semiballoon trawl (2–50 m)	YOY	Oct. 14 – Nov. 4	13–46	18–22	4.3–12.2	11.7–12.2	Wells 1968
		Adult	May 26	13–37	22–31	6.0–13.3	7.8–11.5	
			July 7	9–37	9–13	4.3–10.3	8.4–10.3	
			Oct. 14 – Nov. 4	9–37	13–31	5.7–11.9	10.8–11.8	
Big Sable Point, Saugatuck Ludington	Gill net	Adult	Winter	—	40–50	—	—	Rasmussen 1973
			Spring	—	<10	—	—	
			Summer	—	10–30	—	—	
			Fall	—	30–50	—	—	
Manistique	Otter trawl	YOY	Fall	9–40	18	—	—	Jaiyen 1975
		Adult		40–92	30–60	—	—	
Grand Haven	Otter trawl	YOY	Sept.					Brandt et al. 1980
			Day	—	—	3–18	13–14	
			Night	—	—	3–18	5–6	
		Adults	Day	—	—	7–18	7–16	
			Night	—	—	7–16	11–16	
20 km south of Grand Haven	0.5-m-dia. plantkton net (1–15 m)	Larva	May–Aug.	1–15	4–12	5–23.3	10–16	Tin and Jude 1983

TABLE 5. (*Concluded*)

Lake	Sampling gear (depth sampled)	Life stage	Time of sampling	Distribution of rainbow smelt: Depth (m) Range	Depth (m) Maximum abundance	Temperature (°C) Range	Temperature (°C) Mode	Reference
Cayuga Lake, New York	Gill net (7–110 m)	Adult	July–Sept.	12–55	23–35	4–17	8–10	Galligan 1962
Gull Lake, Michigan	Gill net (0–32 m)	Adult	July	8–28	12–20	10–18	10–11	Burbidge 1969
			Aug.	8–20	10–16	10–14	10–14	
			Oct.	0–28	0–20	10–14	12–14	
			Nov.	0–24	0–20	8–10	10	
Echo Lake, Maine	Gill net (10–18.2 m)	Adult	June	1.5–16.8	9–12.2	—	—	Lackey 1970
			July	1.5–15.2	9–12.2	—	—	
			Aug.	1.5–18.2	9–15.2	—	—	
			Oct.	0–16.8	9–15.2	—	—	
Sakakawea, North Dakota	Gill net 16 locations	Adult	July–Aug.	23–38	—	—	—	Berard 1978
			Aug.	27–38	—	10.8–18.3	—	
Cayuga Lake, New York	Gill net (2–31.5 m)	Adult	June 16	—	—	8.6–12.8	10.0	Dahberg 1981
			July 16	—	—	9.0–19.6	14.0	
			Aug. 18	—	—	10.0–20.6	11.9	
			Sept. 9	—	—	10.1–20.6	10.4	
			Oct. 20	—	—	13.6–14.1	13.8	
Lake Simcoe, Ontario	Gill net (5–30 m)	Adult	Aug.–Sept.	15–30	20–30	8–15	8–10	D. Evans, OMNR, Maple, unpubl. data

Discussion

Characteristics of Lakes Colonized by Rainbow Smelt

With some notable exceptions, rainbow smelt have invaded virtually all of the lake types found in Ontario from shallow to deep, small to large, productive to nonproductive (Secchi 0.5–10.5 m), and having sparse to rich fish communities. Smelt are not reported in any lakes in the LIDB having pH < 6.0 (surface water, May–August), however. This might be significant, since the majority of smelt lakes are found in Algonquin and Northeastern regions of Ontario, areas known to have low buffering capacity in their soils and to be subject to precipitation of low pH (Dillon et al. 1978). Also, Kelso and Minns (1982), using the same data set as us, found about 20% of the surveyed lakes to have surface waters of pH < 6.0. The likelihood, therefore, of smelt having had the opportunity to invade lakes with pH < 6.0 seems high. The tendency of smelt to spawn in streams and on shallow beaches at the time of ice and snow melt might result in their eggs being subject to lethal pH depressions in poorly buffered lakes. Incipient effects of acidity on reproduction of indigenous freshwater fishes in Ontario occur from about pH 4.5 to 6.5 (Harvey 1982; Peterson et al. 1982), suggesting that fish species occurrence in lakes actually colonized by smelt has probably been little affected by acid precipitation.

Rainbow smelt are usually found in lakes considered to be typical of lake trout, that is deep, cold lakes having high transparency and relatively low productivity (Johnson et al. 1977). This corresponds with a higher than expected frequency of occurrence of lake trout (52.9%), lake whitefish (56.6%), and lake herring (55.0%) in lakes inhabited by rainbow smelt. The large mean size of these lakes (52.3 km^2) further explains the species composition in that large lakes suitable for lake trout also tend to have northern pike (*Esox lucius*), walleye, and smallmouth bass (Johnson et al. 1977), species that occur with relatively high frequency in lakes with smelt.

The very high frequency of smallmouth bass (73.3%) in lakes inhabited by smelt probably arises because both species have been widely introduced by humans. Also, smallmouth bass are successful in small, deep, softwater lakes typical of lake trout and large, shallow, hardwater lakes more typical of walleye and northern pike (Johnson et al. 1977). Similarly, higher than expected cooccurrence with pumpkinseed, rock bass, and several cyprinids is probably also due to the common influence of introduction by humans.

Because the primary means of invasion is introduction by humans, the lakes that are most likely to be invaded are those having the greatest access and highest use by cottagers and fishermen. Once an introduction has occurred, the physical–chemical conditions, habitat, and the presence of other fish species presumably determine the success of the invading species. The relative importance of each of these factors is uncertain, smelt being found in a wide variety of lake types, but their frequent occurrence in deep, cool lakes is consistent with their relatively low upper incipient lethal temperature (18°C at 11°C winter acclimation temperature, Thomasson 1963) and the hypolimnetic distribution of adults during summer stratification (Table 5). Knowledge of lake and fish community types in which smelt introductions have failed would provide a better indication of the importance of these factors to the success of smelt populations, but this type of information is rare.

A study of 43 lakes in south-central Ontario (Fig. 1) found that the number of cottages per lake was a function of lake area (log no. cottages = 0.151 + 0.767 log area), with area explaining 68.4% of the total variation (A. McCombie, OMNR, Maple, unpubl. data). Invasion by smelt might therefore simply be a function of the probability of an introduction occurring,

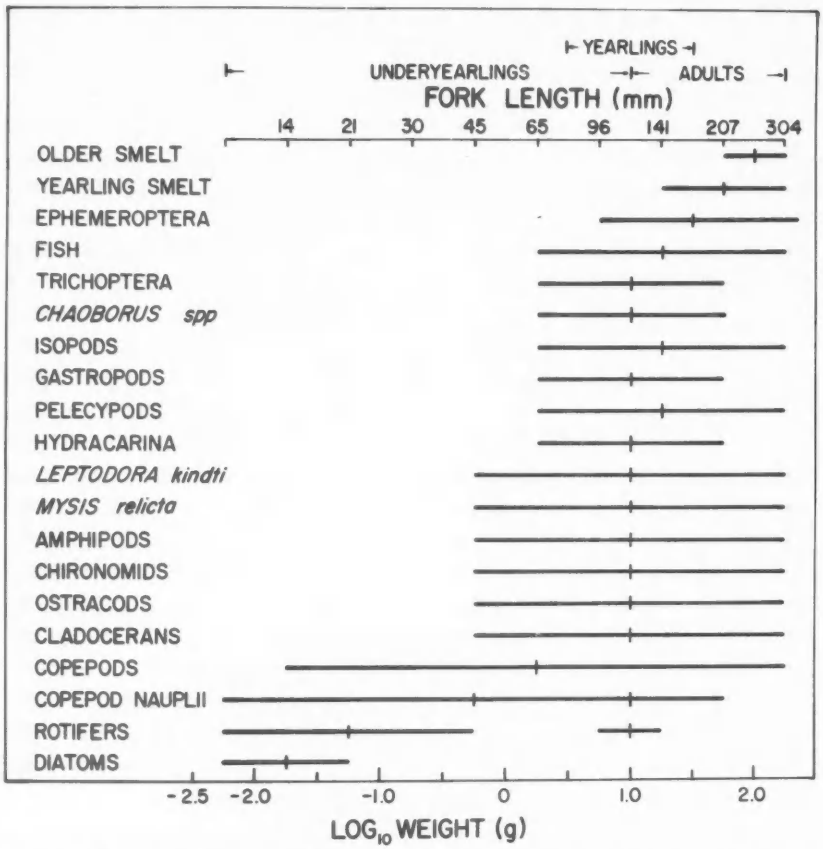

FIG. 2. Occurrence of food item types in smelt stomachs in relation to size of smelt, by size-class. Based on data from Kendall (1927), Creaser (1927), Hale (1959), Price (1963), Siefert (1972), and new data from the Bay of Quinte, Lake Ontario, Lake Simcoe, and Twelve Mile Lake, Ontario (D. O. Evans and D. H. Loftus, unpubl. data). Smelt fork lengths correspond to $\log_{10}$ body weights on the x-axis. Bars indicate the size range over which various items are eaten.

which, in turn, is a function of lake size. An intriguing possibility, however, is that large lakes might also have a greater capacity to accommodate new species, a thesis discussed by Barbour and Brown (1974). They suggested that large lakes might have fewer species than expected because of a shortage of colonists to fill the available habitats.

Lake area has limited capacity to predict the success of an introduction because area alone explains less than 50% of the total variation in species richness in our lake set (Table 1; see also Barbour and Brown 1974). Also, one species could simply be substituted for another, resulting in no change in richness. Species interactions, especially predation, may have a more important bearing on the success of smelt and other exotic invaders. Christie (1974) speculated that declines in stocks of piscivores may, in part, explain the success of exotic planktivores (including rainbow smelt) in the Laurentian Great Lakes.

Species Interactions and Effects of Smelt Introductions

Distribution and case studies of smelt invasions indicate relatively neutral coexistence between rainbow smelt and some species (smallmouth bass, white sucker, yellow perch), harmonious interaction with others, under some circumstances (lake trout, Atlantic salmon, walleye, northern pike, lake herring, emerald shiner), and possibly malevolent interaction under other circumstances (lake whitefish, burbot, walleye, lake trout, lake herring, bloater, alewife). In this section, we examine the detailed species interactions between rainbow smelt and their prey, predators, and competitors for evidence of the mechanisms by which they might affect the abundances of other species.

Smelt as prey

Smelt are utilized as food by virtually all cohabiting piscivores, including larger smelt. They are the major food item of landlocked salmon in Maine lakes (Rupp 1959, 1965; Lackey 1969; Warner 1972; Havey 1973), and following their establishment in the Great Lakes they became important in the diet of lake trout (Schneberger 1936; Hale 1959; Wright 1968). In Lake Superior, the smelt has replaced the bloater as the principal food of the lake trout (Dryer et al. 1965), and they are equally important in the lake trout diet in inland lakes (Bridges and Hambly 1971; MacCrimmon and Pugsley 1979; Hassinger and Close 1984). In the Great Lakes, coho salmon (*Oncorhynchus*

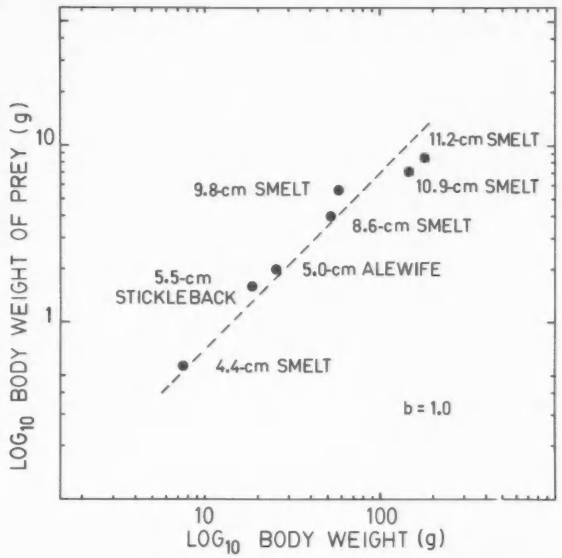

FIG. 3. Relationship between body weight of rainbow smelt and the maximum weight of ingested prey. Based on data from Kendall (1927), Creaser (1927), Hassinger and Close (1984), Stedman and Argyle (1985), and new data from Lake Huron and Twelve Mile Lake, Ontario (D. H. Loftus, unpubl. data). The broken line indicates a slope equal to 1.

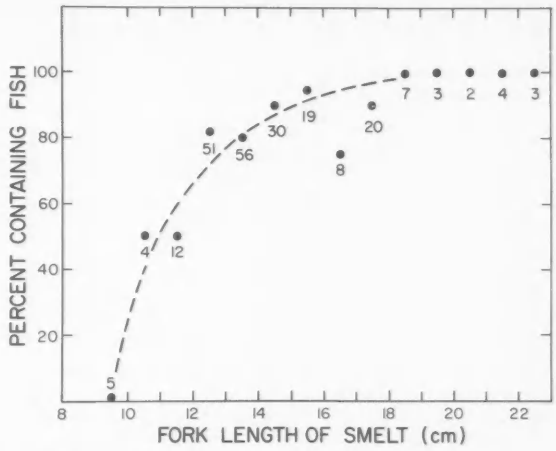

FIG. 4. Frequency of occurrence of fish in stomachs of 225 rainbow smelt containing food in their stomachs in relation to fork length. Smelt were collected in Lake Huron during August and September 1984.

kisutch) and chinook salmon (*O. tshawytcha*) are also major predators of smelt (Stewart et al. 1981; Wismer 1983; Eck and Brown 1985). Rainbow trout (*Salmo gairdneri*), brown trout (*S. trutta*), splake (*Salvelinus fontinalis* × *S. namaycush*), and, to a lesser extent, brook trout (*S. fontinalis*) utilize smelt as well (Lackey 1970; Bridges and Hambly 1971; Eck and Brown 1985). Burbot feed heavily on smelt, especially during spring (Greene 1930; Schneberger 1936; Wagner 1972), as do walleye and northern pike (Greene 1930; Johnson 1963; Wagner 1972; Berard 1978). Other predators include American eel (*Anguilla rostrata*), yellow perch, sauger (*Stizostedion canadense*), white bass (*Roccus chrysops*), white perch (*Morone americana*), and occassionally, rock bass, bowfin (*Amia calva*), lake whitefish, and longnose gar (*Lepisosteus osseus*).

Smith (1970) related that large alewives had been observed feeding on a mixed school of larval smelt and alewives and suggested that alewives could be a major predator on larval smelt in Lake Michigan. In this regard, smelt appear to have disappeared from Big Rideau Lake, Ontario, where alewives have become very abundant. Also, alewives are thought to have caused recruitment failure of smelt in Canadaiqua Lake (Eaton and Kardos 1972).

The effects of changes in smelt abundance on growth rates of predator species have been most obvious in smaller lakes where alternative prey of similar size are lacking. In Schoodic Lake, Maine, for example, Atlantic salmon increased in size following introduction of rainbow smelt, and a subsequent decline in smelt abundance resulted in decreased body condition of the salmon (Havey 1973). Similar responses were observed in Atlantic salmon, brook trout, lake trout, and possibly white perch populations in Quabbin Reservoir, Massachusetts (McCaig and Mullan 1960; Bridges and Hambly 1971). Following the establishment of smelt in West Bearskin Lake, Minnesota, the growth rate of juvenile lake trout was significantly reduced, and the size (and presumably the age) at first maturity increased (Hassinger and Close 1984). In Devilfish Lake, Minnesota, however, the growth rate of trout did not change significantly, but the condition of fish of all ages improved, and size and age at maturity increased (Hassinger and Close 1984). In contrast, Galbraith (1967) observed reduced growth and survival of planted rainbow trout in Sporley Lake, Michigan, following the introduction of smelt.

Predation on smelt by most piscivores in freshwaters indicates that smelt can have a major influence on energy transfer in these systems. In small lakes where smelt are distributed over all depths and habitats, energy sinks, as hypothesized by Christie (1974), are very unlikely to occur. In large, deep lakes, such as Lakes Ontario and Superior, loss of energy to the abyss seems very likely, given the restricted depth distribution of smelt and the absense of the former indigenous ciscoes. Our observations of the distributional and trophic niche dimensions of smelt thus concur with Christie's hypothesis of lost energetic efficiency. In all lakes, however, food web shifts caused by smelt introductions can be expected to cause major restructuring of the fish community.

Smelt as predators

Reif and Tappa (1966) found strong circumstantial evidence that the establishment of smelt in Harvey's Lake, Pennsylvania, resulted in the disappearance of its largest zooplankter (*Leptodora kindtii*) and replacement of *Daphnia pulex* by the smaller *D. dubia*. Galbraith (1967) observed a similar transformation in the zooplankton community of Sporley Lake. In this case, the establishment of smelt and fathead minnows (*Pimephales promelas*) was followed by the complete disappearance of *D. pulex* and an increase in abundance of *D. retrocurva* and *D. galeato mendotae*.

There has been little evidence of reduced abundance of organisms other than zooplankton resulting from predation by smelt, although detailed studies of such "preferred" items as *Mysis relicta, Pontoporeia*, and *Hexagenia* nymphs have not been undertaken. Emerald shiners, for example, apparently have remained abundant in Crystal Lake, Michigan, despite

TABLE 6. Types of food eaten and their relative importance in the smelt diet. Information is from published reports cited in the text.

Plant		
Algae	Occasional	
Animal		
Phylum Rotifera	Occasional	*Asplanchnidae* *Brachionidae* *Testudinellidae*
Phylum Annelida		
Class Oligochaeta	Rare	
Class Hirudinea	Rare	*Helobdella* sp.
Phylum Tardigrada	Rare	
Phylum Arachnida		
Class Hydracarina	Rare	
Phylum Nematoda	Rare	
Phylum Arthropoda		
Class Crustacea		
Order Amphipoda	Very common	*Gamariidae* *Talitridae* *Haustoridae*
Order Cladocera	Very common	*Bosminidae* *Chydoridae* *Daphnidae* *Leptodoridae* *Polyphemidae* *Sididae*
Order Copepoda	Very common	*Centropagidae* *Cyclopidae* *Diaptomidae* *Tremoridae* *Harpacticoida*
Order Mysidacea	Very common	*Mysis relicta*
Order Decapoda	Rare	*Astacidae*
Order Isopoda	Common	*Asellidae*
Order Ostracoda	Common	
Class Insecta		
Order Diptera	Very common	*Ceratopogonidae* *Chaoboridae* *Chironomidae* *Culicidae*
Order Coleoptera	Rare	
Order Ephemeroptera	Common	*Ephemeridae*
Order Hemiptera	Rare	
Order Odonata	Rare	*Aeschnidae*
Order Trichoptera	Rare	
Phylum Mollusca		
Class Gastropoda	Occasional	*Bulimidae* *Planorbidae* *Physidae* *Lymnaeidae*
Class Pelycypoda	Occasional	*Sphaeriidae*
Phylum Chordata		
Class Pisces		
Family Clupeidae	Common	*Alosa pseudoharengus*
Family Salmonidae		
Subfamily Coregoninae	Common	*Coregonus artedii* *C. clupeaformis* *C. hoyi*
Subfamily Salmoninae	Occasional	*Salvelinus namaycush*
Family Osmeridae	Very common	*Osmerus mordax*
Family Cyprinidae	Common	*Notropis hudsonius* *N. atherinoides*
Family Catostomidae	Occasional	*Catostomus commersoni*
Family Gadidae	Occasional	*Lota lota*
Family Gasterosteidae	Occasional	*Pungitius pungitius*
Family Centrarchidae	Rare	*Ambloplites rupestris*

TABLE 6. (*Concluded*)

Family Percidae	Common	*Perca flavescens*
		Etheostoma sp.
Family Cottidae	Occasional	*Cottus cognatus*
		C. ricei
		Myoxocephalus quadricornis
Class Amphibia		
Order Urodela	Rare	

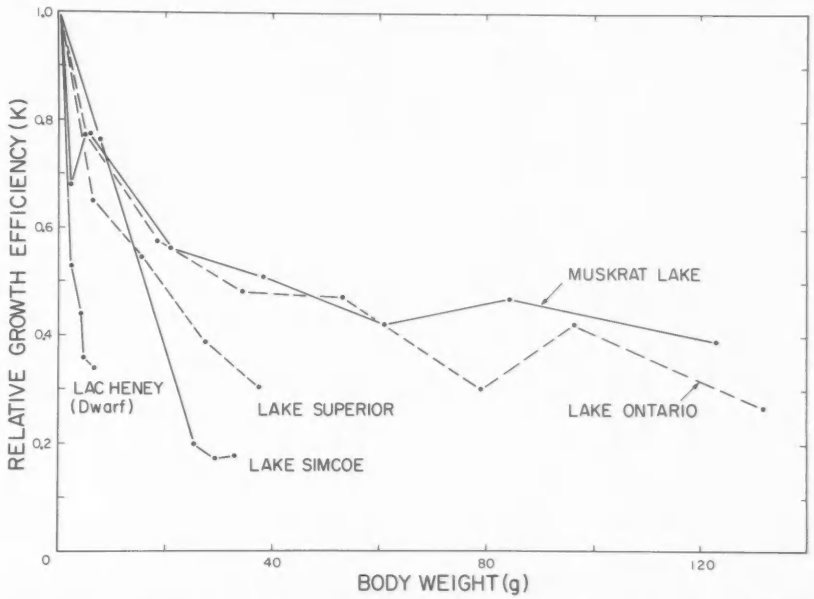

FIG. 5. Relationship between relative growth efficiency [$K_r = \Delta W/(W_i^{0.85} + \Delta W)$] and body weight where W_i is the initial body weight and ΔW is the annual growth increment (Kerr and Ryder 1977). Size at age data: Lac Heney (Delisle 1969), Lake Simcoe (Pugsley 1976), Lake Superior (Schaefer et al. 1981), Lake Ontario (Chen 1970), Muskrat Lake (O'Connor and Power 1974). Data points correspond with annual growth increments.

continuous predation by rainbow smelt since 1912 (Creaser 1925; Beckman 1942). Predation by smelt may have adversely affected recruitment of alewife (O'Gorman 1974) and bloater (Stedman and Argyle 1985) in the Great Lakes, but it has not been possible to establish a cause and effect relationship. Knowledge of the effects of smelt predation on ninespine stickleback (*Pungitius pungitius*), slimy sculpin (*Cottus cognatus*), spoonhead sculpin (*Cottus ricei*), fourhorn sculpin (*Myoxocephalus thompsoni*), darters, and burbot consists of the fact that smelt feed on them to some extent in some situations. In Lac Heney, populations of ninespine stickleback, spoonhead sculpin, fourhorn sculpin, and burbot have apparently persisted in the presence of smelt since the last glacial retreat about 10 000 years B.P. (Delisle 1969).

Lake Huron commercial fishermen reported lake trout eggs and larvae in smelt stomachs in trout spawning areas (Loftus 1980), but Hale (1959) felt that predation on Lake Superior lake trout was probably of little consequence. Loftus and Hulsman (1986) found no evidence of predation on lake trout larvae during spring in Twelve Mile Lake, although given the habitat overlap of young lake trout and adult smelt, and the ability of smelt to consume relatively large prey (Fig. 3), the potential exists for substantial predation of young lake trout (Hassinger and Close 1984). It is certain, however, that lake trout may produce strong year-classes when smelt are present (Bridges and Hambly 1971) and that successful long-standing associations between the two species exist (Kendall 1927; Delisle 1969).

Anderson and Smith (1971) estimated that smelt consumed up to 17% of the herring larvae produced in Nipigon Bay, Lake Superior, where lake herring recruitment was good, but none at all in the Apostle Islands area where recruitment was poor. Crowder (1980) stated that there is strong evidence for interaction between smelt and lake herring in Lake Michigan and felt predation on lake herring may outweigh competition in importance. In Twelve Mile Lake, smelt consumed lake herring and lake whitefish larvae over a period of 7 wk, and up to 28 and 41% of smelt stomachs with food contained these larvae, respectively (Loftus and Hulsman 1986). They concluded that predation by smelt, in combination with other sources of mortality, could explain the recent recruitment failure in lake whitefish in Twelve Mile Lake and that smelt may inflict serious damage on coregonid populations in small lakes where there is a high degree of spatial overlap between the species. In Crystal

TABLE 7. Relative growth efficiency (K_r) at age 4 yr of indigenous and introduced smelt populations in freshwater and marine environments. K_r is calculated as in Fig. 5.

Population	Weight at age 4 (g)	K_r at age 4	Reference
Marine			
Grand Riviere	88.0	0.36	Chen 1970
Miramichi	74.4	0.31	McKenzie 1957
Parker Estuary	70.0	0.14	Murawski and Cole 1978
Freshwater, indigenous			
Bill Lake	55.3	0.58	O'Connor and Power 1974
Lac Heney dwarf	6.5	0.38	Delisle 1969
Lack Heney giant	42.5	0.56	Delisle 1969
Lake Champlain	122.8	0.12	Greene 1930
Matamek Lake	65.4	0.42	Saunders and Power 1970
Mooselookneguntic	61.0	0.35	Rupp 1959
Muskrat Lake	37.9	0.51	O'Connor and Power 1974
Freshwater, introduced			
Crystal lake	56.9	0.02	Beckman 1942
Green Bay	42.5	0.40	Robinson 1973
Lake Erie	28.0	0.23	Sztramko 1984
Lake Ontario	52.6	0.47	Chen 1970
Lake Simcoe	32.6	0.18	Pugsley 1976
Lake Superior	53.9	0.28	Bailey 1964
Lake Superior	37.5	0.31	Schaefer et al. 1981

Lake, however, lake herring and lake whitefish populations coexist with rainbow smelt, and the lake continues to support fisheries for lake whitefish (Laarman 1976). Several other studies (e.g. Kendall 1927; Baldwin 1948; Delisle 1969; MacCrimmon and Pugsley 1979) have also failed to find predation on lake herring by smelt.

Smelt as competitors

Evidence of competition has been largely circumstantial and has consisted of information on habitat and diet overlaps and of changes in growth, survival, and abundance of species associated with smelt. Creaser (1927, 1929) felt that by virtue of their abundance and feeding habits, smelt might be important competitors of lake herring and yellow perch. Anderson and Smith (1971) felt that food competition between smelt and larval lake herring has caused the decline of the lake herring in Lake Superior, although competitive interaction between the two species has not been demonstrated (Lawrie 1978). Hassinger and Close (1984) interpreted a decline in growth of young lake trout in West Bearskin Lake as a response to competition with smelt. Lake Superior smelt share habitat and food with lake trout, but Hale (1959) felt that serious competition did not exist between the two species. Reckahn (1970) concluded that intraspecific competition of young lake whitefish in South Bay, Lake Huron, was probably much more significant than competition with any other fish species, including smelt.

Strong year-classes of whitefish, lake herring, and walleye in Lake Michigan (Wells and McLain 1973) and of whitefish and lake herring in Lake Huron (Berst and Spangler 1973), following the 1942–43 mass mortality of smelt, may have resulted from decreased competition, although environmental factors could possibly have been the cause (Taylor et al. 1987). Declines in walleye abundance have also been associated with increasing smelt abundance, in some cases (Schneider and Leach 1977; Colby et al. 1987; Table 4), but evidence of negative effects of smelt is circumstantial. Complete recruitment failure of lake whitefish occurred in Lake Simcoe during years of peak abundance of smelt and, subsequently, was partly restored when smelt abundance declined (Evans and Waring 1987).

The present structure of the Lake Michigan fish community indicates that considerable reorganization has taken place following the establishment of smelt and alewife (Crowder et al. 1981). Species that declined most rapidly (emerald shiners, lake herring, and deepwater ciscoes (*Coregonus johannae*)) were those with food habits similar to smelt and alewife, but those with different food habits or with the capability of shifting diets (yellow perch, trout-perch (*Percopsis omiscomaycus*), and spottail shiner (*Notropis hudsonius*)) have survived well. Crowder (1980) speculated that smelt probably interact most strongly with lake herring and that predation on young herring may outweigh competition in importance. Christie (1974) noted the collapse of herring stocks following increases in smelt abundance in the Great Lakes. The decline of lake herring in Cayuga Lake, however, has been attributed to alewife rather than smelt (Youngs and Oglesby 1972), and lake herring have produced large year-classes in Lake Simcoe in the presence of high smelt densities (Evans and Waring 1987).

Alewife and smelt appear to be serious competitors for food. Large smelt can consume larger food items than can alewife, but the staple diet of smelt appears to be small invertebrates as it is for alewife (Janssen and Brandt 1980). Rasmussen (1973) observed that in Lake Michigan, the two species utilize similar foods, but that the alewife is the more efficient feeder. In the Great Lakes, smelt have declined in abundance during periods of alewife increases (Smith 1968). Competition with alewife may have resulted in reduced growth of rainbow smelt in New England lakes, and in some cases, smelt may be completely displaced (Eaton and Kardos 1972; Kircheis and Stanley 1981). In the marine environment, alewife and smelt occur in the same areas but are spatially segregated along thermal gradients (Recksiek and McCleave 1973).

Influence of Smelt on Energy Flow in Lakes

Several lines of evidence (case studies of smelt invasions, descriptions of species interactions, growth efficiency relationships, and changes in bioaccumulation of mercury in lake trout) indicate that invasion of indigenous fish communities by rainbow smelt can have major effects on the transfer and storage of energy in these systems.

Our review of case studies revealed changes in growth rates and recruitment success of several species. Cold-water species (lake whitefish, lake trout, lake herring, and Atlantic salmon) were most often affected, as might be predicted on the basis of considerations of niche overlap (Ryder and Kerr 1982). Lake whitefish, the species which frequently declined following smelt invasions, for example, has a life history that is very similar to rainbow smelt, having a pelagic larvae, a demersal, metalimnetic juvenile, and a demersal, hypolimnetic adult (Hart 1930; Kennedy 1943; Reckahn 1970; Hoagman 1973). Smelt and lake whitefish overlap in their use of space and food at each life history stage, resulting in smelt predation on whitefish larvae and possibly competition at all life stages.

One notable feature of the species interactions of smelt in freshwater is the wide spectrum of species and trophic components involved. They feed on zooplankton, larger invertebrates, and small fish, in the water column and on the lake bottom, and

they affect other fish species through resource sharing and predation. Ontogenetic shifts may occur in which smelt eat or compete with the young of species, which as adults prey on larger smelt. Smelt do not simply occupy the same trophic position as indigenous planktivores in freshwater ecosystems. Rather, they are omnivores, feeding across trophic levels, and over three levels of the particle size spectrum of lakes (Sprules et al. 1983). Effects of smelt introductions might, therefore, be expected at several trophic levels, as appears to be indicated by our case studies.

Analysis of relative growth efficiency (K_r) of smelt in freshwater revealed a broad spectrum of realized metabolic niches. The suite of K-lines described (Fig. 5) indicates the full potential from planktivory (Lac Heney) to piscivory (Lake Ontario and Muskrat Lake). Comparison of smelt diet studies in these lakes revealed that relative growth efficiency is positively correlated with the size of prey consumed. We would expect that the potential for smelt to change their pattern of growth by shifting from one K-line to another is great. This would be equivalent to changing from one prey size distribution to a larger one (Kerr and Ryder 1977). Experiments involving transplantation of small smelt to new habitats in several Maine lakes (Rupp and Redmond 1966) confirmed the major influence of environmental factors in controlling growth rates, although sympatric populations of dwarf and normal-size smelt are known (Legault and Delisle 1968; Copeman and McAllister 1978; Lanteigne and McAllister 1983). Different K-lines can reflect not only prey size, but availability of prey as well. For example, intra- and interspecific density-dependent effects on prey availability can often explain changing growth patterns of freshwater fishes (Persson 1983; Hanson and Leggett 1985) within and between lakes. Growth efficiency, therefore, is a reflection of the availability and size of prey, as well as the suitability of the physical environment, for a given species.

Variation in the metabolic niche of smelt in freshwater, as assessed by relative growth efficiency, is taken to mean that differences exist in the scope for activity (includes energy available for growth) in different lakes. We would therefore expect the magnitude of the effects on other species to vary directly with K_r. This may explain the differing effects of smelt introductions between lakes. For example, smelt have continued to coexist with lake whitefish and lake herring, two species thought to be particularly vulnerable to smelt (Smith 1972; Crowder et al. 1981), in Crystal Lake since 1912. Relative growth efficiency of smelt in Crystal Lake is among the lowest we have recorded (Table 7), although it is also relatively low in Lake Simcoe where whitefish recruitment failure coincided with increasing smelt abundance (Evans and Waring 1987).

The size spectrum of prey eaten by smelt increases with smelt body size. Therefore, the potential effects of smelt might be expected to be a function of smelt size. Lanteigne and McAllister (1983) applied this observation in recommending that pygmy smelt be managed as a forage species and that the larger rainbow smelt be managed as a gamefish for winter angling. We would caution against introducing either species in view of the potentially serious effects of rainbow smelt on indigenous species and the risks of misidentifying a small phenotype of the rainbow smelt as the pygmy smelt.

Increased growth rate and body condition of lake trout in inland lakes following smelt introductions indicates redirection of energy flow, and an opposite effect to the energy sink hypothesis proposed by Christie (1974) for large, deep lakes. Increased fat content observed in these lake trout (OMNR, unpubl. data) corresponds with our observation of elevated mercury content of lake trout flesh in lakes inhabited by smelt (OMNR and Ontario Ministry of the Environment 1984a, 1984b). MacCrimmon et al. (1983b) and Wren (1983) also found that the rate of mercury accumulation in the white muscle of lake trout accelerates, as does growth, when lake trout switch to a diet of smelt.

Conclusions

Available evidence indicates that rainbow smelt are well adapted to freshwater, having colonized most lake types available in eastern North America. They are most successful, however, in relatively large, deep lakes inhabited by cold- and cool-water fish species and have not been reported in any Ontario lakes having surface pH < 6.0 (May–August). Smelt are omnivorous in freshwater, their diet varying from small zooplankton to fish up to a maximum prey size of about 6% of their own body weight. As a result, they interact with a wide size spectrum of species and can have a major influence on energy flow and storage in lakes via food web restructuring. The metabolic niche, described here in terms of relative growth efficiency, is highly variable in freshwaters, reflecting, we conclude, differences in the metabolic scope for activity (including growth) as a consequence of food availability and prey size, as well as habitat constraints. Variation in growth efficiency might be related to the variable effects of smelt invasions on indigenous species, although this might also be confounded by intraspecific effects on both growth and recruitment (Evans and Waring 1987).

Few case studies have adequately documented the effects of invasion by rainbow smelt on indigenous freshwater fishes. Recurring observations of declines in lake whitefish populations, however, strongly suggest incompatibility with rainbow smelt, but not in every case. Other species whose growth rates and recruitment appear to be affected in some cases include Atlantic salmon, lake trout, lake herring, walleye, burbot, emerald shiner, alewife, and bloater. While further research is required to understand the apparent inconsistent effects on other species, it is clear that the risks of invasion by rainbow smelt are sufficiently high that managers should attempt to exclude this species from lakes with naturally reproducing stocks of cold- and cool-water species. Specifically, we would recommend against introducing rainbow smelt as prey for lake trout, especially in the case of naturally sustaining stocks, and in softwater areas where bioaccumulation of natural mercury could be accelerated by feeding on smelt. Exclusion of smelt is equally important for the protection of naturally sustaining lake whitefish stocks, especially in small inland lakes (Loftus and Hulsman 1986). Lack of information on the specific effects of smelt on recruitment success of most other species necessitates a cautious management approach.

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Modeling and Management in the Presence of Uncertain Inputs[1]

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Management objectives are often obtained by maintaining a dynamical system at some equilibrium state. It is assumed here that a management program to maintain the system at an equilibrium state has already been specified. However, in the presence of external inputs of an unknown nature, the specified management program is unable to maintain the system in the neighborhood of the equilibrium state. This paper deals with methods for modifying a specified management program so that the system will remain in the neighborhood of the desired equilibrium point in spite of uncertain input. An example is given to illustrate the method.

Les objectifs de la gestion sont souvent atteints par le maintien d'un système dynamique à un certain niveau d'équilibre. On suppose ici qu'un programme de gestion visant à maintenir un système à un niveau d'équilibre donné a déjà été élaboré. Cependant, en présence d'effets externes de nature inconnue, le programme ne permet pas de maintenir le système à une valeur avoisinant l'état d'équilibre. La communication traite de méthodes permettant de modifier un programme de gestion donné de façon à maintenir le système au voisinage du point d'équilibre désiré, ceci en dépit d'effets externes inconnus. La méthode est illustrée à l'aide d'un exemple.

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Differential equation models have been used for many years to describe the dynamics of fish populations. Larkin (1963) used Lotka–Volterra competition equations to describe interspecific competition and exploitation effects in natural fisheries. Parish and Saila (1970) added a modified Volterra predator–prey equation to the two-species Lotka–Volterra competition equations in order to examine Paine's (1966) hypothesis that predation may tend to increase species diversity under some circumstances. They were able to lend support to this hypothesis only under a very special set of parameters. This result demonstrates the importance of considering uncertain effects in system models. Under a certain set of parameters, adding the predator would destabilize an otherwise stable system. Under another set of parameters, adding the predator would tend to stabilize an otherwise unstable system. Clearly, uncertainties either with respect to model parameters and/or the presence of a predator would greatly affect conclusions regarding the stability of this system.

Any ecosystem model will have a degree of uncertainty in its description (May 1974; Beddington and May 1977). There will be uncertainties in the model parameters (carrying capacities, competition coefficients, etc.), as well as uncertainties associated with additional inputs (unknown trophic level effects, unknown environmental effects, etc.). The effects of uncertainty on a system model have previously been investigated. Both stochastic (Ludwig 1975; May et al. 1978) and deterministic approaches (Harrison 1980; Vincent 1981) have been used to evaluate the effects of uncertainty on the dynamics of differential equation system models. It should also be noted that the effects of uncertainties on difference equation models may be obtained using a deterministic approach (Fisher and Grantham 1985). This opens the door to many difference equation models of particular interest in fisheries (e.g. Walters et al. 1980).

The particular emphasis of this paper is to determine management programs for a system defined by differential equations subject to uncertain inputs. The objective of the program is to stablize the system in the vicinity of some desired operating condition in spite of uncertain inputs which may operate to the contrary. A completely deterministic approach is used.

Mathematical Setting

It is assumed that the models of interst may be represented by first-order differential equations of the form

$$\dot{x} = F(x, u) \quad (1)$$

where $F(\cdot)$ is a vector function of the state vector $x = [x_1, \ldots, x_n]^T$ and scalar control u. One is often interested in the management problem of determining a functional relationship for u, such that the system described by (1) will be driven from any initial state to an equilibrium state x* and then be maintained there for all future time.

If (1) is linear in x and u, then the management problem can often by solved by using a linear state variable feedback design of the form

$$u = -h^T x \quad (2)$$

where $h = [h_1, \ldots, h_n]^T$ are appropriate feedback "gains" (e.g. see Brogan 1974). For certain nonlinear ecological systems,

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management by means of constant control is often used (Brower 1981), since the uncontrolled system is already stable. In the latter case, certain long-term management objectives dictate the choice for the constant control (Vincent et al. 1974, 1977).

We will assume here that some sort of state variable feedback management program for the system has already been designed so that, under this control, system (1) may be expressed as

$$\dot{x} = f(x). \tag{3}$$

We also assume that there exists only one desired equilibrium state x^* in some compact specified region X of the state space and that the equilibrium point is asymptotically stable throughout X. It is further assumed that a Liapunov function $V(x)$ is known, such that $V(x^*) = 0$, $V(x) > 0$ for all $x \in X$, $x \neq x^*$ and that

$$\dot{V} = \frac{\partial V}{\partial x} f(x) < 0 \tag{4}$$

for all $x \in X$, $x \neq x^*$.

By design, the control (e.g. equation (2)) which allows (1) to be written as (3) is able to maintain the system at x^* subject to "initial condition" type perturbations. In other words, perturbations which would occasionally move the system in a discontinuous fashion from x^* to some other point in X. Such perturbations are, of course, not modeled by (3) but are readily examined because of the differential equation model. Perturbations of a more persistent nature are perhaps more common than the initial condition type and can only be modeled by modifying equation (3). Examples of this latter type of perturbation would include unpredictable environmental inputs in biological systems (Goh 1976). The ways in which an unknown persistent perturbation can enter into a system are varied. For example, (3) may not model an important trophic level. The interactions from this trophic level affect the dynamics of the system and would appear as an unknown persistent perturbation to the system. Other possibilities include the effect of weather conditions on system parameters assumed independent of such phenomena. Perhaps the simplest way to mathematically express a persistent perturbation which includes these possibilities is by simply adding a perturbing function to the system model (Lee and Leitmann 1983).

Perturbed System

Let s be an unknown persistent perturbation input. Assume that the effect of this input may be modeled by an additive term to equation (3) to obtain

$$\dot{x} = f(x) + g(x)s \tag{5}$$

where $g(\cdot)$ is a vector function of x and $s(t)$ is a scalar piecewise continuous function of time, such that $s_{\min} \leq s(t) \leq s_{\max}$ for all time. Note that the original system (3) is obtained whenever the perturbation input is zero.

Owing to the stable nature of (3), the system will often remain in a neighborhood of the unperturbed equilibrium point x^* in spite of a persistent perturbation. The size and shape of this neighborhood is of interest, and it can often be found or approximated if bounds on the uncertainty are known (Vincent 1981; Fisher and Goh 1981; Grantham 1981). For example, consider the three-species Lotka–Volterra model used by Goh (1977) to demonstrate that local stability of Lotka–Volterra competition models need not imply global stability. This model has also been extensively studied by Pimm (1982). The model is given by

$$\begin{aligned} \dot{x}_1 &= x_1(2 - 0.8x_1 - 0.7x_2 - 0.5x_3) \\ \dot{x}_2 &= x_2(2.1 - 0.2x_1 - 0.9x_2 - x_3) \\ \dot{x}_3 &= x_3(1.5 - x_1 - 0.3x_2 - 0.2x_3) \end{aligned} \tag{6}$$

where x_i represents the population density of species i. This model has a local equilibrium point at (1, 1, 1) which is only locally stable. Suppose now that the dynamics of the third species was not known. However, its effect on the first two, as modeled, was known. We could then represent the system in the form of (5) as

$$\begin{aligned} \dot{x}_1 &= x_1(2 - 0.8x_1 - 0.7x_2) - 0.5x_1 s \\ \dot{x}_2 &= x_2(2.1 - 0.2x_1 - 0.9x_2) - x_2 s \end{aligned} \tag{7}$$

where x_3 has been replaced by s to represent the "unknown" persistent perturbation input. With $s = 0$, the system represented by (7) has a globally stable equilibrium point at (0.569, 2.207). This is illustrated in Fig. 1, which contains a number of system trajectories. Assume that this equilibrium point represents the management objective. Since s represents an unknown third population effect, we have that $0 \leq s \leq s_{\max}$. The value of $s_{\max}$ would not be known according to model (7) and would have to be "estimated." It follows from model (6) than an equilibrium point is given by $x_1 = x_2 = 0$, $x_3 = 7.5$, and thus if x_3 starts out small, a reasonable upper limit is $s_{\max} = 7.5$. The destabilizing effect of this uncertain input may be represented graphically by finding the set of all points reachable from the equilibrium under all possible piecewise continuous functions of time $s(t)$ which satisfy the bounds $0 \leq s \leq s_{\max}$. The fact that s will produce some destabilizing effect is readily seen from (7). At the equilibrium point, each term in parentheses is zero. Thus, any nonzero value for s must produce a change in x_1 and x_2 from the equilibrium values. The extent that the system can be driven away from equilibrium will be a function of the natural stability away from the equilibrium point as well as the magnitude of $s_{\max}$.

The set of points reachable from the equilibrium point under the uncertainty s may be readily calculated using the reachability maximum principle (Grantham and Vincent 1975). According to this principle, if there exists a function $s(t)$ which will drive the system along the boundary of the reachable set, then it must maximize the Hamiltonian function

$$\begin{aligned} H = \lambda_1 x_1(2 - 0.8x_1 - 0.7x_2 - 0.5s) \\ + \lambda_2 x_2(2.1 - 0.2x_1 - 0.9x_2 - s) \end{aligned} \tag{8}$$

at every point of the boundary. The variables λ_1 and λ_2 are adjoint variables which may be thought of as components of an outward-directed normal vector to the boundary of the reachable set. The maximum value of H must also be zero. It is not difficult to show that for this problem the maximum principle yields just two possibilities for boundary control, which are $s = 0$ and $s = s_{\max}$. The reachable sets illustrated in Fig. 2 were obtained using these two boundary controls. First, starting at the unperturbed equilibrium point, the system is driven to a new equilibrium point using $s = s_{\max}$. Then, from this new equilibrium point, the system is returned to the unperturbed equilibrium point using $s = 0$. The resultant trajectories trace out the boundary of the reachable set for a given value of $s_{\max}$. It may be readily verified through additional numerical computation that the sets so obtained are indeed the reachable sets.

The lower right corner point of each of the reachable sets in Fig. 2 corresponds to an equilibrium solution of (7) with $s =$

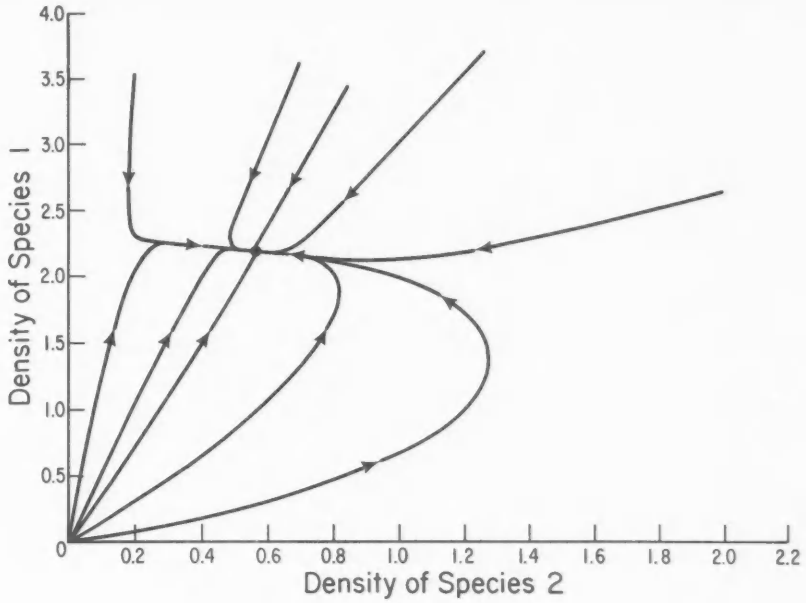

FIG. 1. Two-species equilibrium.

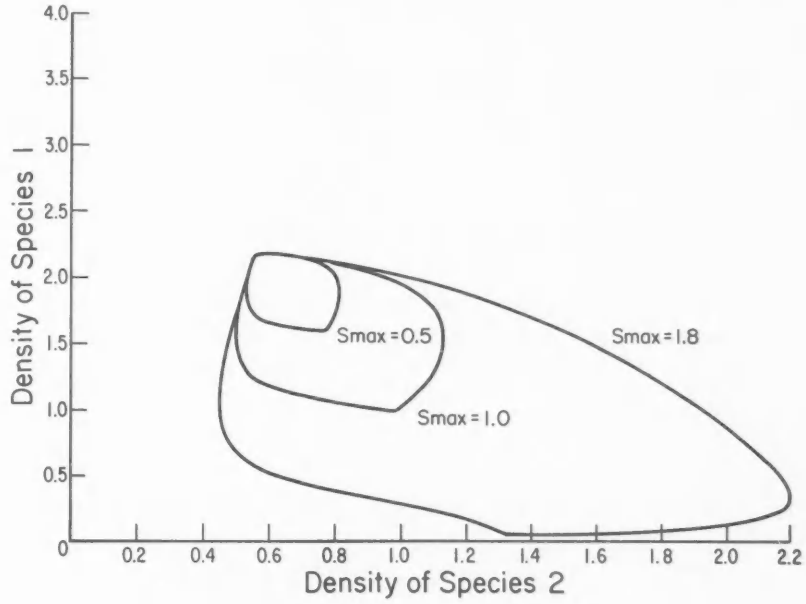

FIG. 2. Two species with uncertain input s.

s_{max}. By setting $\dot{x}_1 = \dot{x}_2 = 0$ and eliminating s in (7), we obtain the line

$$1.4x_1 + 0.5x_2 = 1.9. \quad (9)$$

All equilibrium points must lie on this line, and we obtain an equilibrium point on the x_1 axis with $s_{max} = 1.828$. Note that this value for s_{max} is much less than the limit of $s_{max} = 7.5$.

The two-species system is thus very vulnerable with respect to the third species. Figure 3 illustrates the effect of starting the system at the two-species equilibrium point and at a point near the three-species equilibrium point. In both cases, $x_3(0) = 0.5$ and the trajectories are determined by integrating (6). The trajectory from the two-species equilibrium point results in extinction for both species 1 and 2. The trajectory in the neigh-

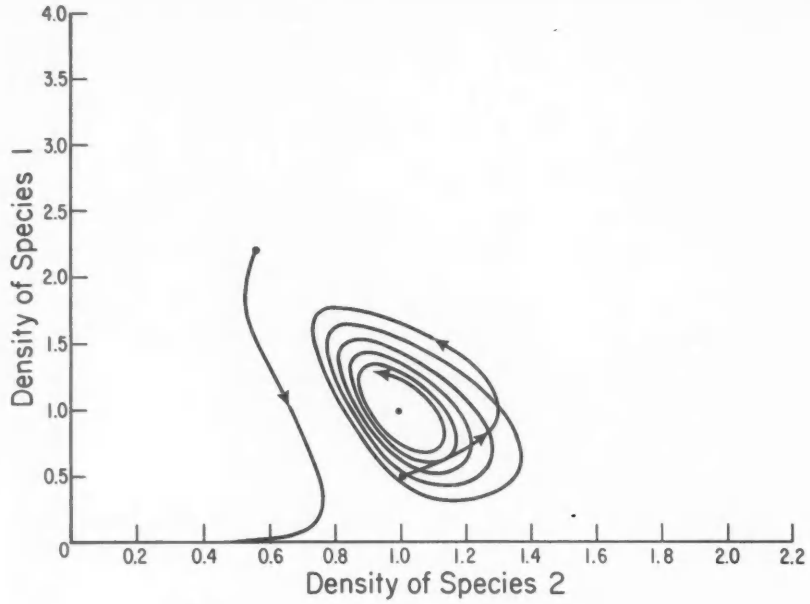

FIG. 3. Two species with a third species as the uncertain input.

borhood of the three-species equilibrium point illustrates the weak stability of this point. Note that the trajectory can cross itself, since Fig. 3 represents a projection of the three-dimensional system onto the two-species space. It would appear that a severe management challenge is represented if we attempt to maintain the system at the two-species equilibrium point. Clearly, the reachable set under the "unknown" perturbation is not acceptable due to the large value for s_m.

Controlling the Perturbed System

The "second method" of Liapunov is often used to provide a general approach to the design and analysis of control systems (Kalman and Bertram 1960). Leitmann (1983) has further developed this type of analysis for use with systems subject to uncertainty. Lee and Leitmann (1983) made use of a previous result obtained by Corless and Leitmann (1981) to stabilize systems of the form (5). Vincent et al. (1985) have also examined this system using a combined reachable set/Liapunov analysis. We will use similar methods here for the determination of a management program to deal with system uncertainty.

Assume that an additional scalar control p may be added to equation (5) in a manner similar to the uncertain input, so that the controlled system becomes

$$\dot{x} = f(x) + g(x)s + h(x)p \tag{10}$$

where $h(\cdot)$ is a vector function of x. Consider now the time derivative of the Liapunov function associated with system (3) under the dynamics of system (10):

$$\dot{V} = \frac{\partial V}{\partial x} f(x) + \frac{\partial V}{\partial x} g(x)s + \frac{\partial V}{\partial x} h(x)p. \tag{11}$$

At the equilibrium state x^*, the derivative $\partial V/\partial x = 0$, which implies that $\dot{V} = 0$. This does not imply that an input for s cannot drive the system away from the equilibrium point. The second time derivative of V is given by

$$\ddot{V} = \frac{\partial V}{\partial x}\left(\frac{\partial f}{\partial x} + \frac{\partial g}{\partial x} s + \frac{\partial h}{\partial x} p\right)(f + gs + hp) + (f + gs + hp)^T \frac{\partial^2 V}{\partial x^2}(f + gs + hp). \tag{12}$$

Since $\partial V(x^*)/\partial x$ and $f(x^*) = 0$, it follows that at the equilibrium point x^*

$$\ddot{V} = (gs + hp)^T \frac{\partial^2 V}{\partial x^2}(gs + hp). \tag{13}$$

Since V takes on an ordinary proper local minimum at x^*, it follows that $\ddot{V} < 0$ whenever $gs \neq -hp$. Without the additional control input p, any small disturbance will drive the system away from the equilibrium point. Even with an additional control input, movement away from the equilibrium point should be expected, since p cannot usually be chosen to satisfy $gs = -hp$. The problem now is to choose a control law for p so that movement away from the equilibrium point under the uncertainty s will be confined to a neighborhood of the desired equilibrium point x^*.

If we choose a control law for p of the form

$$p = -k\left(\frac{\partial V}{\partial x} h\right) \tag{14}$$

where k is a constant gain to be determined, then (11) becomes

$$\dot{V} = \frac{\partial V}{\partial x} f(x) + \frac{\partial V}{\partial x} g(x)s - k\left(\frac{\partial V}{\partial x} h(x)\right)^2. \tag{15}$$

By (4), the first term on the right-hand side of (15) is negative, and by our choice for p, the last term is also negative. The objective is to find a value for k so that $\dot{V}$ will be guaranteed

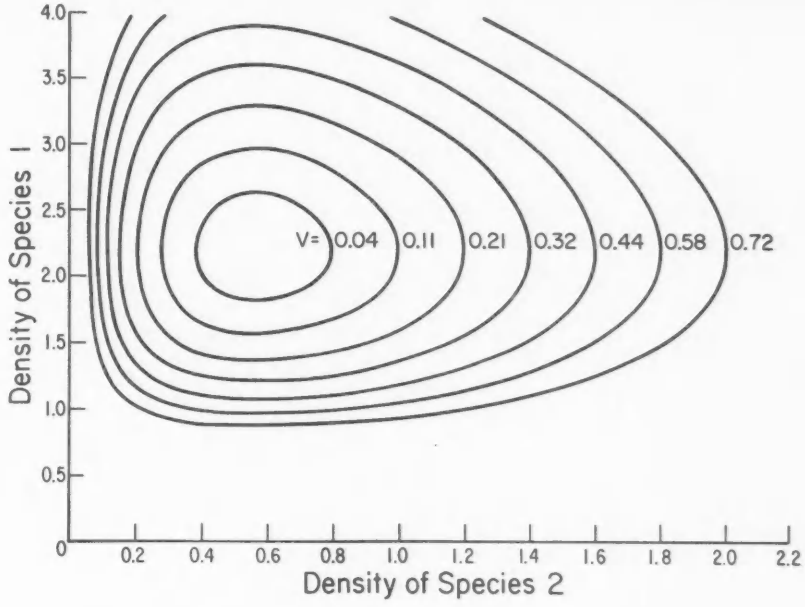

FIG. 4. V-level curves.

negative outside of some region about the equilibrium point. Toward this end, define

$$(16)\quad s_m = \max\,[|s_{\min}|, |s_{\max}|].$$

It follows from (15) that whenever

$$(17)\quad \left|\frac{\partial V}{\partial x}\, g(x)\right| s_m \leq k\left(\frac{\partial V}{\partial x}\, h(x)\right)^2$$

for any $x \neq x^*$, the derivative $\dot{V}$ will be less than zero. Consider now all points $x \in X$ for which

$$(18)\quad \left|\frac{\partial V}{\partial x}\, g(x)\right| s_m > k\left(\frac{\partial V}{\partial x}\, h(x)\right)^2.$$

It follows from (15) that

$$(19)\quad \dot{V} \leq \frac{\partial V}{\partial x}\, f(x) + \left|\frac{\partial V}{\partial x}\, g(x)\right| s_m.$$

If there exists a neighborhood about the origin so that all points outside the neighborhood satisfy

$$(20)\quad \frac{\partial V}{\partial x}\, f(x) \leq -\left|\frac{\partial V}{\partial x}\, g(x)\right| s_m$$

whenever

$$(21)\quad k\left(\frac{\partial V}{\partial x}\, h(x)\right)^2 < \left|\frac{\partial V}{\partial x}\, g(x)\right| s_m$$

then this neighborhood defines a region within which the system is guaranteed to remain under the uncertainty and additional control action. Conditions (20) and (21) simplify somewhat if $g(x) = h(x)$. In this case, (20) is replaced by

$$(22)\quad \frac{\partial V}{\partial x}\, f(x) \leq -\frac{s_m^2}{k}$$

and (21) is replaced by

$$(23)\quad \left|\frac{\partial V}{\partial x}\, h(x)\right| < \frac{s_m}{k}.$$

In the latter case, condition (22) will often by satisfied if the region defined by (23) corresponds to a region of strong natural system stability.

Application to the Lotka–Volterra Model

Consider again the example problem under "Controlling the Perturbed System." A Liapunov function for (7) with $s = 0$ is given by Goh (1980):

$$(24)\quad V(x_1x_2) = x_1 - x_1^* - x_1^* \ln \frac{x_1}{x^*} + x_2 - x_2^* - x_2^* \ln \frac{x_2}{x_2^*}$$

where $x_1^* = 0.569$ and $x_2^* = 2.207$. The function V is valid throughout the region X defined by

$$(25)\quad X = \{x \in E^2 | x_1 > 0 \text{ and } x_2 > 0\}.$$

Various level curves for the function (23) are illustrated in Fig. 4.

The components of the gradient are given by

$$(26)\quad \frac{\partial V}{\partial x_1} = 1 - \frac{x_1^*}{x_1}$$
$$\frac{\partial V}{\partial x_2} = 1 - \frac{x_2^*}{x_2}.$$

It follows from (7) that

$$(27)\quad g(x) = \begin{bmatrix} -0.5x_1 \\ -x_2 \end{bmatrix}.$$

Assume that the additional control is introduced so that $h(x) =$

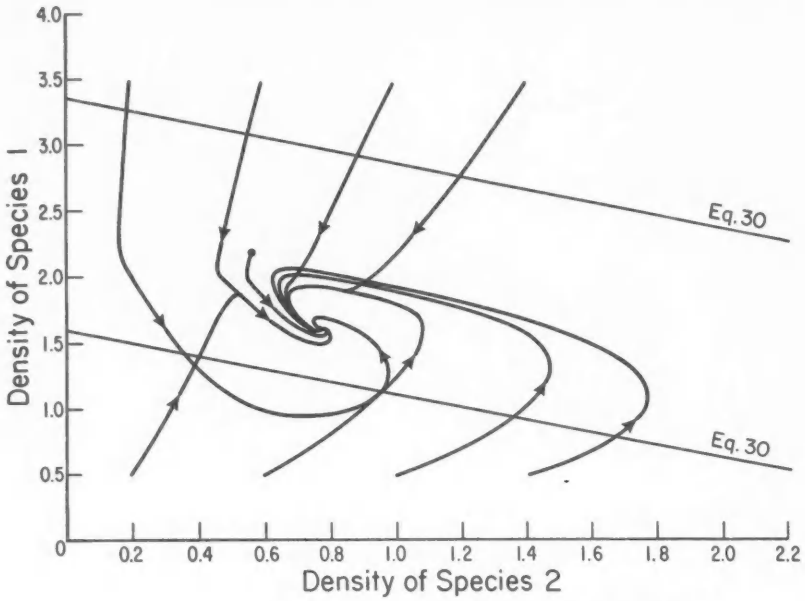

FIG. 5. Two species with x_3 uncertain input and additional control.

$g(x)$. Thus, the controlled system becomes

$$\begin{aligned}\dot{x}_1 &= x_1(2 - 0.8x_1 - 0.7x_2 - 0.5s - 0.5p)\\ \dot{x}_2 &= x_2(2.1 - 0.2x_1 - 0.9x_2 - s - p).\end{aligned} \tag{28}$$

We obtain the control law for p from (14) to obtain

$$p = k[0.5(x_1 - x_1^*) + (x_2 - x_2^*)]. \tag{29}$$

Our objective is to choose a value of k to maintain the system in the neighborhood of x^*. Since $h(x) = g(x)$, we can use (22) and (23) as a guide for making this choice. First we can estimate s_m by setting $\dot{x}_3 = 0$ in (6) and solving for x_3 with x_1 and x_2 equal to the two-species equilibrium values. This yields $s_m = 1.34$. Of course, if the dynamics of species three is actually not known, then s_m would have to be estimated by some other means. If we choose $k = 1.5$, then $\dot{V}$ is guaranteed to be less than zero whenever

$$|0.5(x_1 - x_1^*) + (x_2 - x_2^*)| > \frac{s_m}{k} > 0.89. \tag{30}$$

We should expect to maintain the system in a neighborhood of the origin somewhat smaller than this.

Figure 5 illustrates the dynamics of (28) under the additional control (29) with the uncertainty s drive by the x_3 equation of system (6) and with $x_3(0) = 0.5$. In this case, we maintain system stability with respect to a new equilibrium point in the neighborhood of x^*. System trajectories from a number of starting points (including x^*) are illustrated. Trajectories can cross, since this figure is a two-dimensional projection of the three-dimensional system. The region defined by (30) is also illustrated in Fig. 5. Note that the new equilibrium point is well within this band.

If we include the dynamics of the uncertainty with equations (28) (i.e. replace s with x_3 and include the $\dot{x}_3$ equation from (6)) along with the additional control as provided by (29), then the dynamics represented in Fig. 5 is given by

$$\begin{aligned}\dot{x}_1 &= x_1[(2 + 0.25kx_1^* + 0.5kx_2^*)\\ &\quad - (0.8 + 0.25k)x_1 - (0.7 + 0.5k)x_2 - 0.5x_3]\\ \dot{x}_2 &= x_2[(2.1 + 0.5kx_1^* + kx_2^*)\\ &\quad - (0.2 + 0.5k)x_1 - (0.9 + k)x_2 - x_3]\\ \dot{x}_3 &= x_3(1.5 - x_1 - 0.3x_2 - 0.2x_3).\end{aligned} \tag{31}$$

With $k = 1.5$, the equilibrium solution of (0.7736, 1.6338, 1.1813) is obtained. The first two components of this equilibrium solution are the equilibrium solutions obtained in Fig. 5. At this equilibrium point, a constant additional control is required. From (29) we obtain $p = 0.70635$. Note that the equilibrium uncertain input of $s = 1.1813$ was somewhat less than our original estimate.

Increasing the gain k will move the controlled equilibrium point closer to x^*. However, this in turn will increase the steady-state requirement for p.

If s were a bounded random input rather than an input determined by the $\dot{x}_3$ dynamics, then the reachable set under s for the system (28)–(29) can be determined as illustrated in Fig. 6. Note that the equilibrium point x^* is unchanged with the application of the control given by (29). Comparing Fig. 2 and 6, it is noted that the system is now less vulnerable to the uncertainty. Compare in particular the curves corresponding to $s_{max} = 1.8$ (Fig. 2) and $s_{max} = 2$ (Fig. 6). The region defined by $s_{max} = 1$ (Fig. 6) is in close agreement with the result obtained in Fig. 5, in spite of the fact that the bounds on the uncertainty used in Fig. 5 were potentially much larger than $s_{max} = 1$.

Since the uncertainty in this example could never have negative values, the additional control law as given by (29) is in some cases more than required. This observation suggests modifying the control law so that $p = 0$ when additional control is not

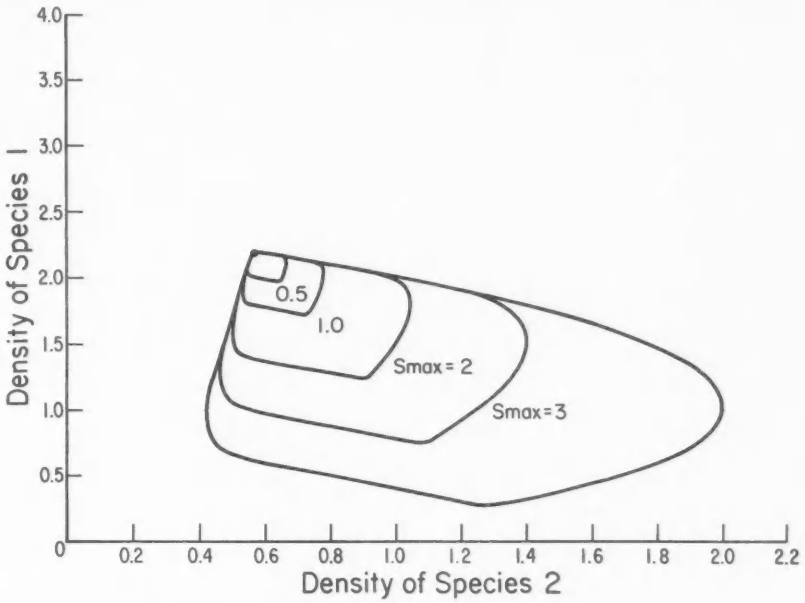

FIG. 6. Two species with bounded uncertain input and additional control.

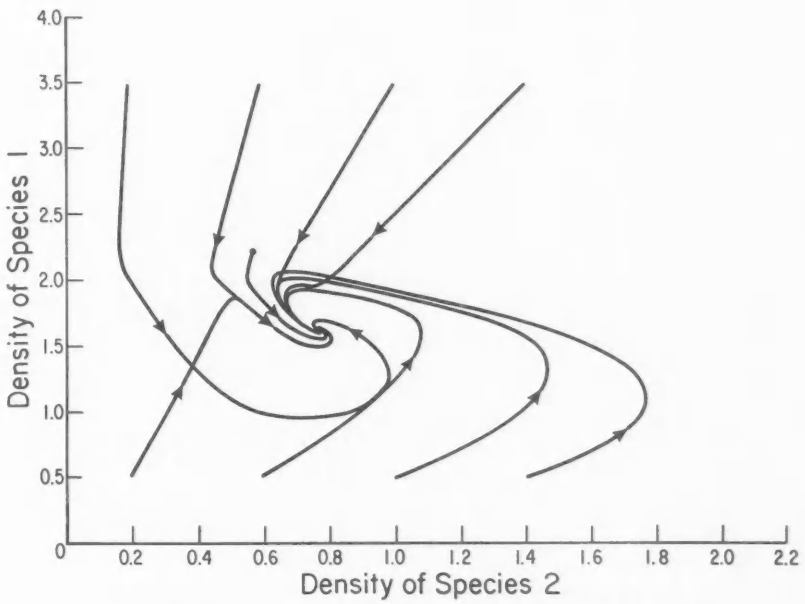

FIG. 7. Two species with uncertain input and modified additional control.

needed. It follows from (11) that if $s \geq 0$, then whenever

$$(32) \quad \frac{\partial V}{\partial x}\, g(x) \leq 0$$

we may set $p = 0$, since the natural dynamics in this case will assure $\dot{V} < 0$. Since $g = h$ in this example, if we define

$$(33) \quad \sigma = 0.5(x_1 - x_1^*) + (x_2 - x_2^*)$$

then the control law for p as given by (29) may be replaced by

$$(34) \quad \begin{aligned} &\text{If } \sigma > 0, \text{ then } p = k\sigma \\ &\text{If } \sigma \leq 0, \text{ then } p = 0. \end{aligned}$$

Figure 7 illustrates the results obtained under this control law using the dynamics provided by (28) with s replaced by x_3 and including the $\dot{x}_3$ equation from (6). By comparing Fig. 7 with

Fig. 5, we note that while there might be a considerable savings in control, the dynamics of the two systems differ very little and the end result is the same. Any savings in control would, of course, depend on starting conditions.

Discussion

Environmental systems are subjected to both "initial condition" and "persistent" types of perturbations. The former type of perturbation may be thought of as being brought about from time to time by singular events. The traditional regulator control design deals with such events by simply providing equilibrium point stability throughout X. The persistent type of perturbations is thought of here in terms of continuous uncertain inputs.

A nonzero persistent perturbation of the type modeled by (5) will always cause some destabilization of the system in the vicinity of the equilibrium point. If the uncertainty is bounded, then the extent of its destabilizing effect can be determined by using the reachability maximum principle to find the boundary of the set of points reachable under the uncertainty. For one- and two-dimensional systems, the determination of the reachable set using the reachability maximum principle is not difficult. However, for higher dimensional systems, the reachability maximum principle is difficult to apply, and the best one may be able to do is estimate the reachable set by other methods (Grantham 1981; Gayek 1984). In any event, a reasonable estimate of the reachable set should suffice for determining whether the potential destabilizing effect of the uncertain input is "acceptable." If it is not, then some additional control measures must be employed in order to contain the effects of the uncertainty.

There are a number of ways of doing this, and other methods besides the one presented here have been offered. These include methods based on worst case analysis (Ragade and Sarma 1967; Vincent 1980) and methods based on the "second" method of Liapunov (Corless and Leitmann 1981; Lee and Leitmann 1983; Vincent et al. 1985). The advantage of the particular method used here is that it can "adapt" to unknown limits on the uncertainty and requires very little additional control effort if the uncertainty is such that the system should remain in the vicinity of the desired equilibrium point.

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Biomass Dynamics of Lake Superior Lake Herring (*Coregonus artedii*): Application of Schnute's Difference Model[1,2]

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Jacobson, L. D., W. R. MacCallum, and G. R. Spangler. 1987. Biomass dynamics of Lake Superior lake herring (*Coregonus artedii*): application of Schnute's difference model. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 275–288.

Schnute's (1985. Can. J. Fish. Aquat. Sci. 42: 414–429) difference model was used to study the biomass dynamics of lake herring (*Coregonus artedii*) in Thunder Bay and Black Bay, Lake Superior, during 1948–79. Recruitment to both fisheries appeared to be independent of escapement during previous years. Abundance of lake herring in Black Bay varied without trend during the study period despite a strong peak in effective fishing effort during 1968–70 and a general trend of increasing effort throughout the study period. Abundance of Thunder Bay lake herring declined during 1948–50 and 1959–67 and increased when fishing effort declined. The estimated catchability coefficient for small-mesh gill nets (54–83 mm stretched measure) set in Black Bay for lake herring during November was $0.467/10^2$ km net. The estimated catchability coefficient for small mesh gill nets set in Thunder Bay for lake herring during December was $0.132/10^2$ km net. Estimates of natural mortality rates and recruitment levels for both fisheries were confounded and unreliable. This analysis demonstrates the utility of Schnute's model for management of Great Lakes herring stocks and some difficulties with its application.

Les auteurs ont utilisé le modèle des différences de Schnute (1985. Can. J. Fish. Aquat. Sci. 42: 414–429) pour étudier la dynamique de la biomasse du cisco de lac (*Coregonus artedii*) dans les baies Thunder et Black (lac Supérieur) pour la période 1948–1979. Le recrutement chez les deux espèces semblait indépendant de l'échappée au cours des années précédentes. Dans la baie Black, l'abondance du cisco a varié sans tendance pendant la période étudiée malgré une forte poussée de l'effort de pêche effectif de 1968 à 1970 et une tendance générale vers une augmentation de l'effort de 1948 à 1979. Dans la baie Thunder, le nombre de ciscos a baissé de 1948 à 1950 et de 1959 à 1967 pour ensuite augmenter quand l'effort de pêche a diminué. Le potentiel de capture des filets maillants à petites mailles (ouverture de 54 à 83 mm) mouillés en novembre dans la baie Black pour la pêche du cisco a été estimé à $0{,}467/10^2$ km de filets, et à $0{,}132/10^2$ km de filets pour ceux mouillés en décembre dans la baie Thunder. Les estimations des taux de mortalité naturelle et des niveaux de recrutement chez les deux espèces n'étaient pas claires et donc douteuses. La présente analyse montre l'utilité du modèle de Schnute pour la gestion des stocks de cisco peuplant les Grands Lacs et certains des problèmes d'application.

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This paper describes an analysis of the biomass dynamics of lake herring (*Coregonus artedii*) in Black Bay and Thunder Bay, Lake Superior, during 1948–79. The class of population dynamics models used in this analysis is based on difference equations that were developed originally by Deriso (1980) and elaborated by Schnute (1985). Our intention was to determine the utility of these models for management and analysis of Great Lakes fish stocks. In principle, these models can be used to (1) estimate the range of sustainable yields for a fishery, (2) forecast short-term changes in abundance of fish, (3) determine trends in abundance, (4) estimate quantities of general interest (e.g. catchability coefficients and recruitment parameters), and (5) make inferences about growth, recruitment, and mortality in the stock.

Schnute's general model is quite similar to the model developed by Deriso (1980) except that growth and mortality are represented in a more general fashion (Schnute 1985). Tyler et

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al. (1985) use a simulation experiment to show that Deriso's model provides a good approximation to the population dynamics of an age-structured fish population under exploitation. An analogous experiment has not been performed using Schute's model. We are confident, however, that Schnute's model is at least as capable of tracking the biomass dynamics of an actual fish stock because of similarities between the two models and because Schnute's model includes Deriso's as a special case. A disadvantage of Schnute's general model, which might be important when catch and effort data are limited, is that Schnute's model includes a time lag that is 1 yr longer than the time lag in Deriso's model. Consequently, an extra year of data are available for parameter estimation when Deriso's model is used. All of the parameters in Schnute's models can, in principle, be estimated from catch and effort data.

All of the parameters in Schnute's models are familiar to fisheries biologists and represent a concrete biological process or entity. As a result, parameter estimates can often be obtained from information other than the catch and effort data. We call information of this sort "auxiliary information" after Deriso et al. (1985). Auxiliary information is important because it is difficult to obtain satisfactory estimates of a large number of parameters from a single series of catch and effort data. Furthermore, it is often useful to compare estimates of parameters obtained from catch and effort data to values obtained by other means.

An important characteristic of Schnute's (1985) model is flexibility; he described 24 variations of the basic equation. We expect, furthermore, that managers and scientists will be able to make modifications of their own in order to construct models that are appropriate for particular fisheries. Surplus production (Schaefer 1954; Pella and Tomlinson 1969), yield-per-recruit (Ricker 1975), and autoregressive models (Deriso 1980; Roff 1983) are special cases of Schnute's basic model (Schnute 1985). The important point is that Schnute's general model can be tailored, with relative ease, to suit the fishery and data to which it is applied.

The approach to modeling and analysis of fish populations that Schnute (1985) advocates is important. He suggested that the analyst initially select the variation or group of variations of the basic model that are most appropriate for the stock under consideration. Model identification is then an iterative process of fitting individual models and rejecting those that are unsuitable. We subscribe to this general approach and have used these techniques in the analyses described below.

Problems with Analysis of Data from Great Lakes Fisheries

Periods of stability are virtually unknown in Great Lakes fisheries; changes in the fisheries themselves complicate modeling and analytical efforts. Changes in efficiency of fishing gear (Pycha 1962), stocking (Lawrie and MacCallum 1980), establishment of exotic species (Lawrie and Rahrer 1973), pollution (Hartman 1973), and changes in regulations all complicate analysis and interpretation.

A number of workers have used models to assess the status and estimate potential yields of Great Lakes fish stocks (Silliman 1969; Sakagawa and Pycha 1971; Jensen 1976, 1978; Patriarche 1977; Walters et al. 1980; Goodier and Spangler 1981; Selgeby 1982; Koonce et al. 1983). Each of these previous efforts suffered, to varying degrees, from inadequate data. Long time series of catch and effort data are difficult to obtain for most fisheries even though commercial catch and effort statistics have been collected since 1950 by Ontario and all states bordering the Great Lakes (Hile 1962). The format, condition, and accessibility of commercial fishing information confound analysis and modeling of Great Lakes fish stocks. The quality of commercial fishing data that are available is usually unknown and questionable (Hartman and Ross 1985). Some errors in tabulations of commercial fishing data have been corrected, at considerable expense, by reexamining commercial fishing reports (MacCallum 1984). We believe that integrity and accessibility of commercial fishing data are issues that have received insufficient attention from managers of Great Lakes fisheries.

Synopsis of Relevant Life History

Lake herring are pelagic planktivores found during the summer scattered across the open waters of Lake Superior. Spawning occurs in November and December at which time herring aggregate in relatively shallow water such as that found in Black Bay and Thunder Bay. Spawning is apparently promiscuous, eggs are deposited pelagically and hatch the following spring. Van Oosten (1929), Dryer and Beil (1964) and Smith (1956) give more complete descriptions of the life history of lake herring.

The Fisheries

Lake herring are exploited commercially in Black Bay and Thunder Bay mainly during the spawning season (MacCallum and Selgeby 1987). An important characteristic of this fishery is that fishing mortality occurs just before spawning; females invariably contain eggs when harvested (Selgeby 1982). Gill nets, pound nets, trap nets, and trawls were used to harvest lake herring. Selgeby (1982) described the nature, history, and collapse of lake herring fisheries in the Wisconsin waters of Lake Superior.

Stock Structure

In this analysis we assume that lake herring from Thunder Bay and Black Bay belong to different stocks. The two fisheries are managed as though the stocks are separate, and patterns in catch-per-unit-effort for the two fisheries differ substantially (Fig. 1 and 2). There is, however, no proof that two different stocks exist. Black Bay and Thunder Bay are separated only by the Sibley Peninsula (Fig. 3). Lake herring spend a portion of the year on the open waters of Lake Superior where they may mix freely. Lake herring are not known to "home" at spawning time. These facts suggest that lake herring from Thunder Bay and Black Bay may belong to the same stock. Our analysis is not valid if Thunder Bay and Black Bay lake herring belong to the same stock; more complex models that reflect the interrelationship between the two fisheries would be required for a satisfactory analysis.

Materials and Methods

Assignment of Ages

In order to use notation consistent with that of Deriso (1980) and Schnute (1985), ages of lake herring were assigned so that a fish of age k in year t is the result of spawning in year $t - k$. The life of a herring is assumed to begin at the egg stage and ages are incremented on January 1 regardless of the chronological age of

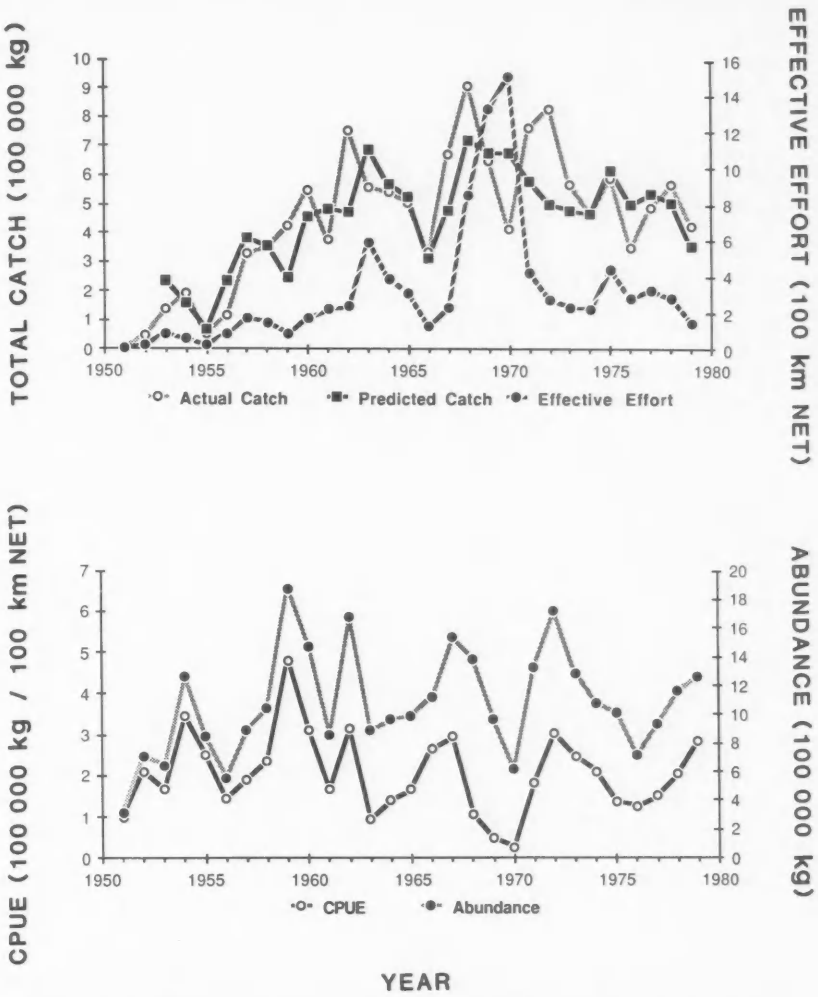

FIG. 1. Upper: observed and predicted catch of lake herring (in 10^5 kg round weight) and total effective effort (in 10^2 km small-mesh gill net lifted) for Black Bay during 1951–79; lower: abundance (in 10^5 kg) at beginning of the year and November CPUE (in 10^5 kg/10^2 km small-mesh gill net lifted) for Black Bay lake herring age V and older during 1948–79. Abundance was calculated as the catch-per-unit-mortality according to Schnute (1985, eq. 2.5).

the fish. For example, lake herring age I in January of 1980 would be the result of spawning during November or December of 1979.

Form of the General Model

To begin the analysis, we used the general model designated <111> Schnute (1985, eq. 2.8):

$$C^*_{t+1}/(1-\phi_{t+1}) = (1+\rho)\tau_t C^*_t/(1-\phi_t) - \rho\tau_t\tau_{t-1}C^*_{t-1}/(1-\phi_{t-1}) + V_{t+1-k}R_{t+1}\{S_{t+1-k}\} - \rho\tau_t v_{t-k}R_t\{S_{t-k}\}$$

where C^*_t = total weight of the catch in year t, ϕ_t = fraction of population extant at the beginning of year t that is not caught by the fishery (see below), $C^*_t/(1-\phi_t) = N^*_t$ = total biomass of stock extant at the beginning of year t (note that $C^*_t = (1-\phi_t)N^*_t$), τ_t = fraction of population extant at the beginning of year t that survives to the beginning of year $t+1$ (see below), k = age at recruitment to the fishery, ρ = Ford's growth coefficient (Ricker 1975, p. 222), V_t = weight of individual fish at age k (at recruitment) in year t, v_t = weight of individual fish at age $k-1$ (1 yr prior to recruitment) in year t, S_t = escapement biomass in year t, $= \phi_t C^*_t/(1-\phi_t)$, since $N^*_t = C^*_t/(1-\phi_t)$ and $S_t = \phi_t N^*_t$, and $R_t\{\ \}$ = recruitment function (gives numbers of fish, not biomass) for year t. We use the same notation as Schnute (1985).

Since fishing mortality occurs during a brief period at the end of the year just prior to spawning, we used eq. 1.11c and 1.12c in Schnute (1985) to calculate ϕ_t and τ_t:

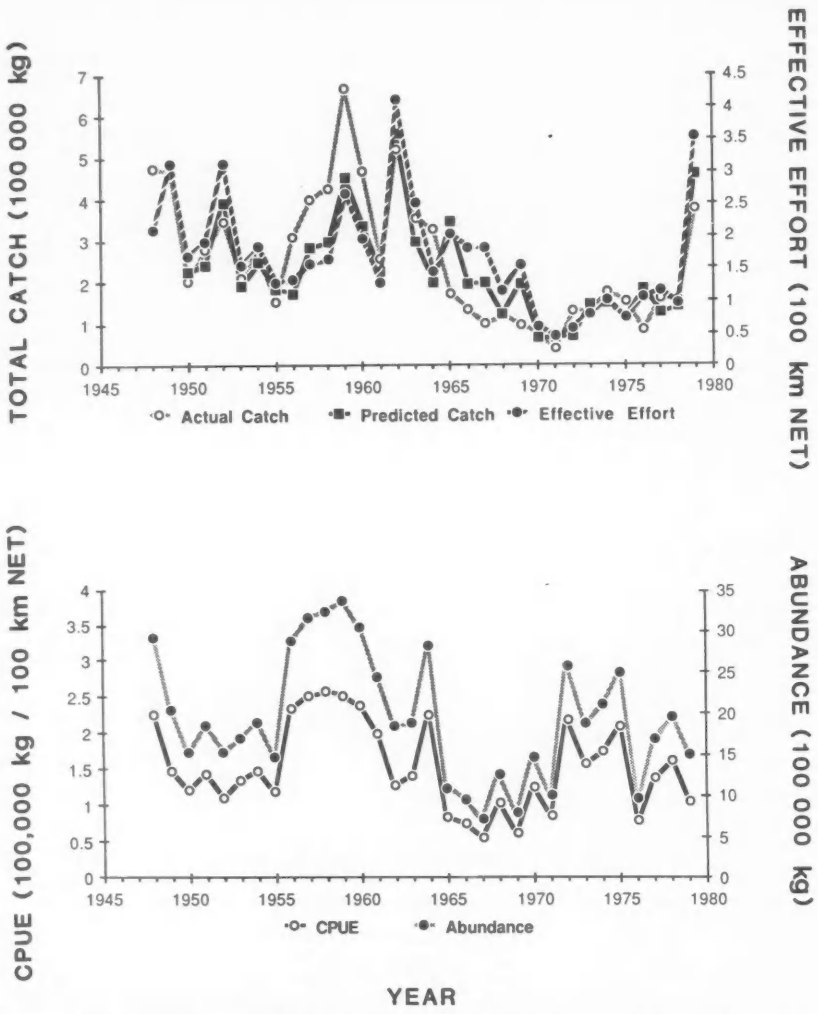

FIG. 2. Upper: observed and predicted catch of lake herring (in 10^5 kg-round weight) and total effective effort (in 10^2 km small-mesh gill net lifted) for Thunder Bay during 1948–79; lower: abundance (in 10^5 kg) at beginning of the year and December CPUE (in 10^5 kg/10^2 km small-mesh gill net lifted) for Thunder Bay lake herring age V and older during 1948–79. Abundance was calculated as the catch-per-unit-mortality according to Schnute (1985, eq. 2.5).

$$\sigma_t = \{1 + \exp(qE_t)[\exp(M) - 1]\}^{-1}$$

$$\phi_t = 1 - \exp(-M)[1 - \exp(-qE_t)]$$

$$\tau_t = \sigma_t \phi_t$$

where σ_t = fraction of population extant at the beginning of year t that is not caught by the fishery and does not succumb to natural mortality in year t, q = catchability coefficient (a constant), E_t = fishing effort in year t, and M = instantaneous rate of natural mortality (a constant). The assumptions required to derive model <111> are as follows: (1) Complete recruitment occurs at age k. (2) recruitment in year $t + 1$ is a function of escapement biomass ($\phi_{t+1-k}N^*_{t+1-k} = N^*_{t+1-k} - C^*_{t+1-k}$) in year $t + 1 - k$. This assumption is a bit subtle; in reality some lake herring not caught by the fishery will die of natural causes and fail to spawn. (3) All fish age k or older are sexually mature. (4) The natural mortality rate for fish age k and older is constant over time. (5) Natural and fishing mortality rates are the same for all recruited age classes. (6) Natural mortality occurs first and is followed by a pulse of fishing mortality at the end of the year just prior to spawning. (7) Growth of individual fish can be described by eq. 1.9 in Schnute (1985):

$$w_{a+1,t+1} - w_{a,t} = \rho(w_{a,t} - w_{a-1,t-1})$$

where $w_{a,t}$ is the weight of an individual fish at age a in year t. Units for all parameters are given in Table 1.

It is worth noting that the assumption of constant natural mortality is probably valid for lake herring. Natural mortality of many Great Lakes fishes cannot be assumed constant because of predation by sea lamprey (*Petromyzon marinus*) during its inva-

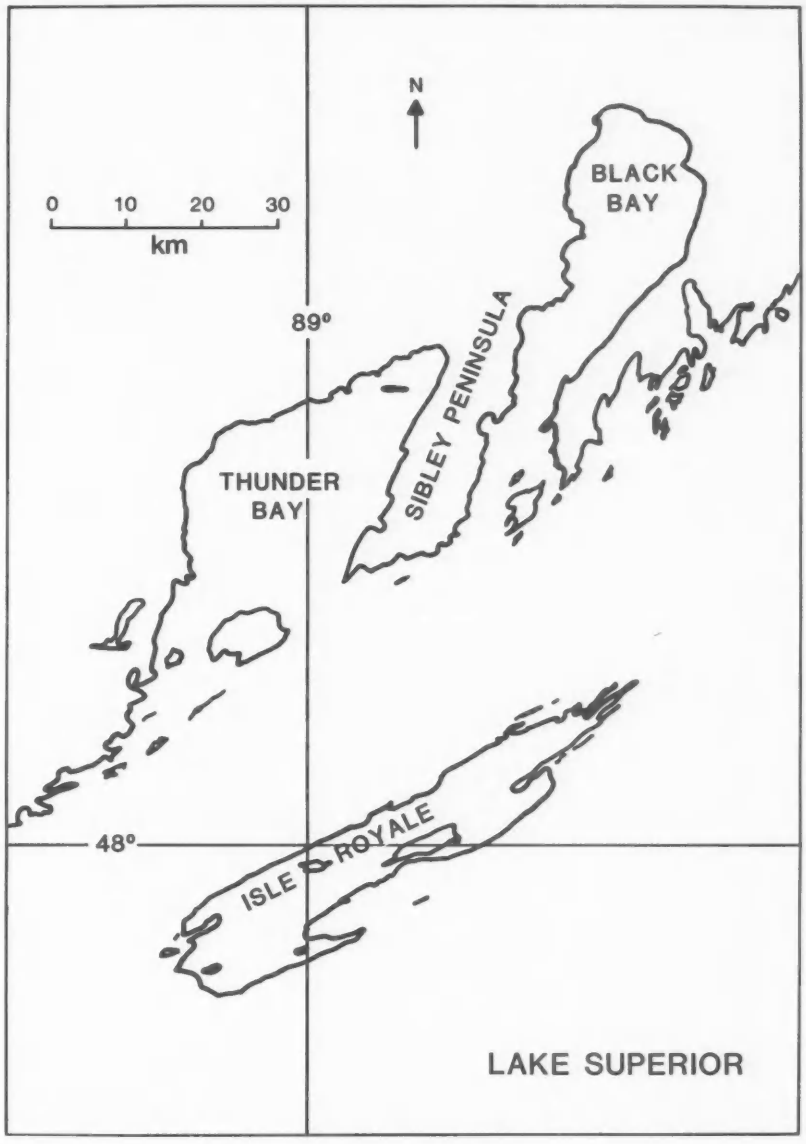

FIG. 3. Thunder Bay and Black Bay, Lake Superior.

sion, increase in numbers, and eventual reduction in numbers due to a successful program for sea lamprey control (Smith and Tibbles 1980). Lake herring, however, are not known to experience significant mortality due to predation by sea lamprey. Christie and Kolenosky (1980, table 1) reported that lamprey wounding rates for lake herring in Lake Ontario during 1954–63 were 0.57 marks/100 fish as opposed to 3.95 marks/100 fish for lake whitefish (*Coregonus clupeaformis*) and 35.6 marks/100 fish for lake trout (*Salvelinus namaycush*) during the same period. It is likely that the effects of sea lamprey predation on mortality of lake herring were minimal.

The assumption of "knife-edge" recruitment at age k can be relaxed if a modification to model <111> proposed by C. Walters (Institute of Animal Resource Ecology, University of British Columbia, 2075 Westbrook Place, Vancouver, B.C. V6T 1W5, pers. comm.) is employed. This modification involves two assumptions: (1) fish recruit to the fishery immediately on reaching a particular weight (V) rather than at a particular age and (2) at each age a fixed proportion (π_a where a is the subscript for age) of the total recruitment from every cohort attains weight V and recruits to the gear. Recruitment in year $t + 1$ is given by

$$R_{t+1} = \sum_{a=j}^{k} \pi_a R\{S_{t+1-a}\}$$

TABLE 1. Units and descriptions for parameters and symbols.

Parameter	Description	Units
k	Age of full recruitment	Years
ρ	Ford's growth coefficient	—
V	Weight at recruitment	10^5 kg/fish
v	Weight 1 yr prior to recruitment	10^5 kg/fish
q	Catchability coefficient	$(10^2$ km net$)^{-1}$
M	Instantaneous coefficient for natural mortality	—
R_m	Recruitment parameter (asymptotic recruitment in model <111>, constant recruitment in model <114>)	Fish
δ	Recruitment parameter for density dependence	10^5 kg
π_a	Proportion of each cohort that recruits at age a	—
λ	Importance of residual from year t in the prediction of catch for year $t+1$	
ϵ_0	Residual for year prior to the first year in the data series	ln (10^5 kg)

where j is the first age at which fish attain weight V and recruit to the gear, k is the age at which all fish are fully recruited to the gear, and $R\{\ \}$ is a recruitment function with parameters that are constant from one year to the next. The disadvantage in this modification is that extra parameters (π_a for $a = j$ to k) must be estimated. An advantage is that models with one parameter (π_k) are nested within (submodels of) models with two parameters (π_{k-1}, π_k), and so on. The necessity for including any particular age-class in the recruitment calculations can be evaluated by using a likelihood ratio test (described below) to determine if the appropriate parameter (e.g. π_{k-1} for age-class $k-1$) is significantly different from zero. We used Walter's modification in our analysis but limited the number of age-classes over which recruitment occurs to two in order to minimize the number of parameters estimated. Note that the π_a must sum to unity so that only one extra parameter must be estimated when recruitment is spread over two age-classes. In our analysis, $\pi_{k-1} = 1 - \pi_k$.

Schnute's (1985) recruitment function has three parameters. In order to reduce the number of recruitment parameters, we assumed that a Beverton and Holt type recruitment curve (Ricker 1975, p. 291) was appropriate for lake herring. The form of the true recruitment relationship for herring is unknown. In the absence of direct information, it is reasonable to assume that production of recruits from Black Bay and Thunder Bay would eventually rise to an asymptote as the biomass of spawners increased. Although lake herring eat their own eggs (Dryer and Beil 1964), the emerging larvae and adults are spatially separated. It seems unlikely that cannibalism of young by adults (Ricker 1975, p. 281) is sufficient to result in a domed Ricker type recruitment curve.

J. Schnute (Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, pers. comm.) suggested the following parameterization of the Beverton and Holt curve:

$$R\{S_{t+1-a}\} = R_m/(1 + \delta/S_{t+1-a})$$

where R_m and δ are parameters. Note that recruitment is a constant (R_m) when δ is zero. When δ is not zero, recruitment depends on the biomass of spawners and approaches R_m asymptotically as spawner biomass increases. The advantage in this modification is that the constant recruitment model described by Schnute (1985, eq. 3.6) is nested in the more general model <111>. The hypothesis that recruitment depends on spawner biomass can be addressed by using a likelihood ratio test to determine whether or not the estimate of δ is significantly different from zero. We used Schnute's parameterization of the Beverton and Holt curve in our analysis.

The Constant Recruitment Model

The constant recruitment model (designated <114> by Schnute 1985) provides a useful alternative to the general model <111> when there is no evidence of a relationship between stock size and recruitment. An advantage of model <114> is that there are no time lags due to recruitment so that additional years of data are available for parameter estimation. There are two principle disadvantages. First, it is impossible to estimate the range of sustainable yields from the parameters in model <114>. Second, and most importantly, the parameter estimates for natural mortality (M) and recruitment (R_m) tend to be highly correlated and grossly imprecise when both estimates are obtained from catch and effort data. Correlations between estimates for M and R_m in model <114> have often, in our experience, approached unity. We have not been able to determine if this problem is due to the structure of the constant recruitment model or the data with which we have worked. It appears difficult, however, to obtain satisfactory estimates for either of these parameters unless the value of one can be obtained from auxiliary information.

Age at Recruitment

Catch curves for lake herring harvested commercially from Black Bay during 1965–73 (data from Goodier 1981, p. 256–258) were examined to determine the age of full recruitment to the fishery. Lake herring appeared to be fully recruited to the Black Bay fishery by age VI although substantial numbers of age V fish were also caught (ages assigned in the manner described above). Catch curves for lake herring harvested commercially from four areas along the south shore of Lake Superior (Dryer and Beil 1964) during 1950–59 were also examined. Herring along the south shore appeared to be fully recruited to the gear by age V. We chose to use age V as the age at which recruitment is complete because we were aware of problems with aging of fish in the data for Black Bay and because an additional year of data are available for parameter estimation when age V is used.

TABLE 2. Catch and effort data for Black Bay lake herring. Catch in units of 10^5 kg round weight; effort in units of 10^2 km of small-mesh (54–83 mm stretched measure) gill net lifted. The correction factors were used to adjust November CPUE for changes in efficiency of small-mesh gill nets. Effective effort is the total catch divided by the corrected November CPUE.

Year	Total catch	November catch	November effort	Correction factor	Effective effort
1951	0.048	0.011	0.026	0.455	0.050
1952	0.482	0.427	0.401	0.509	0.230
1953	1.398	1.077	1.149	0.564	0.840
1954	1.929	1.857	0.868	0.618	0.557
1955	0.511	0.339	0.200	0.673	0.203
1956	1.177	0.843	0.808	0.727	0.821
1957	3.254	1.922	1.285	0.782	1.701
1958	3.486	2.321	1.171	0.836	1.471
1959	4.228	2.259	0.528	0.891	0.880
1960	5.481	4.725	1.596	0.945	1.750
1961	3.737	3.217	1.949	1.000	2.264
1962	7.527	3.744	1.187	1.000	2.386
1963	5.602	1.476	1.552	1.000	5.888
1964	5.431	2.859	2.043	1.000	3.881
1965	5.046	1.643	0.996	1.000	3.058
1966	3.346	0.906	0.341	1.000	1.260
1967	6.703	1.680	0.569	1.000	2.269
1968	9.072	1.249	1.170	1.000	8.499
1969	6.485	0.210	0.430	1.000	13.299
1970	4.120	0.550	2.012	1.000	15.070
1971	7.620	0.727	0.399	1.000	4.181
1972	8.269	1.078	0.355	1.000	2.723
1973	5.684	0.783	0.317	1.000	2.302
1974	4.698	1.058	0.505	1.000	2.241
1975	5.896	0.795	0.589	1.000	4.369
1976	3.489	0.402	0.323	1.000	2.801
1977	4.895	0.978	0.648	1.000	3.243
1978	5.687	1.053	0.520	1.000	2.808
1979	4.233	1.299	0.456	1.000	1.487

Catch and Effort Data

The catch and effort data used in this analysis (Tables 2 and 3; Fig. 1 and 2) were taken from various summaries produced by the Ontario Ministry of Natural Resources from monthly reports submitted by commercial fishermen working in Black Bay and Thunder Bay. All catch and effort data for 1948–60 were taken from a recent retabulation of the original commercial fishing reports (MacCallum 1984). Total catch data for 1961–79 (Black Bay) and 1961–71 and 1973–79 (Thunder Bay) were taken from routine annual summaries. An effort was made to correct the 1961–79 catch data for trawl catches from Black Bay that were mistakenly assigned to Thunder Bay. Total catch from Thunder Bay during 1972 was taken from Goodier (1981, p. 261–278) because the figure obtained from the annual summary (about 7000 kg) seemed too low. December catch and effort data for small-mesh gill nets (54–83 mm stretched measure) set in Thunder Bay during 1961–79 were taken from Goodier (1981, p. 261–278) as were November catch and effort data for small-mesh gill nets set in Black Bay during the same period. Goodier and Spangler (1981, p. 10–11) discussed corrections to these data.

The catch and effort data available from different sources for some years differed substantially. The figures used in this analysis were, in our opinion, the best available. The catch and effort data for 1948–60 obtained from the retabulated summaries are probably the best information obtainable from the commercial fishing reports. The quality of the data for 1961–79 is less certain.

The model requires values for total catch and total effort. No direct measure of total effort is available, however, because several types of gear are used and catch is occasionally reported without information about effort. We estimated total effective effort by dividing the total catch by catch-per-unit-effort (CPUE) (Gulland 1969, p. 53–54) after the CPUE was corrected for changes in efficiency of the gear (see below). The estimate of CPUE that we used was the total catch with reported effort by small-mesh gill nets divided by the total reported effort for small-mesh gill nets. November CPUE values were used to estimate effective effort for Black Bay because there was no reported catch from Black Bay for December in some years. December CPUE values were used to estimate effective effort for Thunder Bay because there was no reported catch from Thunder Bay for November in some years. Effort data were scaled to units of 10^2 km of small-mesh gill net lifted, and catch data were scaled to units of 10^5 kg for the remainder of the analysis.

The efficiency of small-mesh gill nets used to harvest lake herring changed when the twine used to make gill nets was changed from linen and cotton to multifilament nylon. Selgeby (1982) discussed the change from cotton and linen gill nets to nylon gill nets in the Wisconsin herring fishery during 1951–61 and reviewed estimates of the relative efficiency of nylon gill nets. We assumed that the period of conversion was the same for

TABLE 3. Catch and effort data for Thunder Bay lake herring. Catch in units of 10^5 kg round weight; effort in units of 10^2 km of small-mesh (54–83 mm stretched measure) gill net lifted. The correction factors were used to adjust December CPUE for changes in efficiency of small-mesh gill nets. Effective effort is the total catch divided by the corrected December CPUE.

Year	Total catch	December catch	December effort	Correction factor	Effective effort
1948	4.730	3.477	3.386	0.455	2.094
1949	4.630	2.696	3.996	0.455	3.120
1950	2.041	1.865	3.391	0.455	1.687
1951	2.768	1.034	1.578	0.455	1.919
1952	3.458	0.863	1.527	0.509	3.113
1953	2.102	1.271	1.669	0.564	1.555
1954	2.726	1.472	1.608	0.618	1.839
1955	1.540	0.929	1.157	0.673	1.291
1956	3.105	2.286	1.346	0.727	1.329
1957	3.974	2.413	1.223	0.782	1.574
1958	4.239	2.606	1.210	0.836	1.646
1959	6.680	3.265	1.456	0.891	2.654
1960	4.660	3.534	1.573	0.945	1.961
1961	2.559	1.081	0.544	1.000	1.288
1962	5.200	2.130	1.683	1.000	4.109
1963	3.557	2.812	1.984	1.000	2.510
1964	3.289	0.956	0.422	1.000	1.450
1965	1.722	1.119	1.319	1.000	2.030
1966	1.367	0.252	0.335	1.000	1.812
1967	1.020	0.649	1.155	1.000	1.815
1968	1.192	0.889	0.860	1.000	1.153
1969	0.984	0.774	1.223	1.000	1.557
1970	0.759	0.622	0.498	1.000	0.608
1971	0.394	0.295	0.341	1.000	0.456
1972	1.295	0.107	0.048	1.000	0.589
1973	1.264	0.732	0.461	1.000	0.795
1974	1.776	0.719	0.411	1.000	1.017
1975	1.550	1.080	0.514	1.000	0.737
1976	0.849	0.163	0.204	1.000	1.062
1977	1.631	0.725	0.520	1.000	1.171
1978	1.591	0.838	0.515	1.000	0.977
1979	3.770	1.371	1.282	1.000	3.526

Black Bay and Thunder Bay, that multifilament nylon gill nets were 2.2 times more efficient than cotton or linen gill nets (Dryer and Beil 1964), and that the conversion to multifilament nylon gill nets occurred at a constant rate between 1951 and 1961. Correction factors (Tables 2 and 3), based on these assumptions, were used to compute the adjusted CPUE:

$$c' = c/\zeta$$

where c' is adjusted CPUE, c is observed CPUE, and ζ is the correction factor.

Unpublished data provided by W. MacCallum suggest that efficiency of gill nets towards lake herring increased as fishermen in Black Bay and Thunder Bay switched to deeper nets (more meshes vertically) and from multifilament nylon to monofilament nylon net twine during the period 1961–79. We did not correct the effective effort and CPUE data for these changes, however, because there was too little information about the magnitude of the change in gill net efficiency.

Estimation of Growth Parameters

Back-calculated lengths at age for lake herring from Michigan waters of Lake Superior during 1950–59 (Table 4) were obtained from Dryer and Beil (1964, table 25) and used to compute growth parameters for our model (ρ, V_t, and v_t). Unpublished data provided by W. MacCallum suggest that growth of lake herring in Thunder Bay and Black Bay changed during 1948–79. It was impossible to obtain estimates of growth parameters from these data, however, because the fish were not aged reliably. The growth parameters in the models that we used were assumed to be constant because we could not determine how much the growth of lake herring had changed. Dryer and Beil's (1964) data were obtained, roughly, in the middle of our study period and should provide a good estimate of typical or "average" values for growth parameters during the study period.

A modified version of the length–weight relationship for lake herring reported by Dryer and Beil (1964) was used to convert total lengths to round weights:

$$W = 0.0000028329L^{3.17008}$$

where W is round weight in grams and L is total length in millimetres.

Weight at age data were plotted and, since the plot was linear, a straight line was fitted to the data by least squares. The regression line was

$$W = -96.584 + 49.615A$$

where W is round weight in grams and A is age in years. Note that a linear relationship between weight at age and age implies

TABLE 4. Total length and round weight at ages II–IX for Lake Superior lake herring. Back-calculated lengths at age were obtained from Dryer and Beil (1964, p. 514, table 25). Values for length shown below are mean values for samples collected from four areas along the south shore of Lake Superior during 1950–59. Weights were calculated from lengths according to: $W = 0.0000028329L^{3.17008}$ where weight (W) is in grams and length (L) is in millimetres (modified from Dryer and Beil 1964, p. 509).

Age	Total length (mm)	Round weight (g)
II	119.38	10.87
III	186.51	44.72
IV	236.58	95.05
V	277.59	157.76
VI	298.99	199.65
VII	321.13	250.38
VIII	340.72	302.10
IX	356.87	349.86

that the parameter ρ in Schnute's growth model is equal to 1. The linear regression model fitted the data very well (R^2 = 99.8%).

Lake herring caught during the November and December spawning season have completed all of their growth for that year. The regression equation predicts weight at the beginning of the year. The weights of ages IV and V lake herring caught during the spawning season were therefore taken to be the predicted weights of ages V and VI from the regression equation. Predicted weights for lake herring age V and age VI were 151.5 and 201.1 g, respectively. Values of 1.515×10^{-6} and 2.011×10^{-6} were used for the parameters v and V (units are 10^5 kg) in the remainder of the analysis.

Estimation of Other Parameters

Parameter values other than those describing growth (M, q, R_m, δ, π_k, and π_{k-1}) were estimated by nonlinear regression analysis (Draper and Smith 1981). Both sides of model <111> (modified as described above) were multiplied by $(1 - \phi_{t+1})$ so that catch in year $t + 1$ was expressed as a function of catch and effort in previous years. Parameters were estimated by regression of catch data on catch and effort data according to the modified model. Appropriate terms for statistical error were introduced as described below.

Estimates of the correlations among parameter estimates were obtained as described in Draper and Smith (1981, p. 472–473). This method gives approximate estimates because it is based on a linear approximation to the nonlinear regression model.

Nonlinear regression algorithms attempt to find parameter estimates that minimize the sum of the squared differences between observed and predicted values of the independent variable. This approach is familiar because it is the same approach used to estimate parameters in linear regression problems. An important difference between linear and nonlinear regression is that parameters in nonlinear models can be very difficult to estimate. Nonlinear regression problems involving the models described by Schnute (1985) and Deriso (1980) are often "ill-conditioned." It may be difficult to find the solution (set of parameter estimates) that gives the best fit of the model because many solutions give almost identical sums of squares for error. There may be a large number of "local" minima in the sum of squares surface that prevent algorithms from finding the true "global" minimum and best parameter estimates. Parameter estimates may be highly correlated, imprecise, and biased. Draper and Smith (1981, p. 487–488) and Ratkowsky (1983, p. 5–7) discussed these problems.

It is true that least squares estimates obtained by nonlinear regression are maximum likelihood estimates when residuals are normally and independently distributed about their expected value. Consequently, if the sample size is very large, parameter estimates should be unbiased, normally distributed, and have minimum variance. It is not clear, however, how large the sample must be in order to obtain these desirable characteristics, and series of catch and effort data for fisheries are usually short. Ratkowsky (1983, p. 6) suggested that a least squares estimate of a parameter in a nonlinear model "has essentially unknown properties for finite sample sizes." Uncertainty about the properties of estimates is further compounded by error in the measurement of independent variables (catch and effort) and the possibility that residuals are not independent (see below). Deriso (1980) emphasized the desirable, asymptotic properties of least squares parameter estimates for nonlinear models. We think it more informative to emphasize the problems and uncertainties that analysts must face when they estimate parameters in nonlinear models such as those developed by Deriso (1980) and Schnute (1985).

Our experience suggests that problems with parameter estimation can be minimized by (1) using models with as few parameters as possible, (2) obtaining as many parameter estimates as possible from auxiliary information, and (3) correcting fishing effort data for changes in efficiency where appropriate. Constraints on parameter estimates may help the analyst avoid impossible solutions (e.g. mortality rates can be constrained to be larger than zero). In order to determine if a set of parameter estimates is a global solution, it is helpful to fit the same model several times starting with different initial values for parameters. We found it most convenient to use software that did not require specification of partial derivatives.

Statistical Error

Statistical errors in the models described above can be additive or multiplicative; Schnute (1985) discussed reasons for assuming one or the other. We observed that variance of residuals was more nearly constant when multiplicative errors were assumed. For this reason, both sides of our models were log-transformed before parameters were estimated by nonlinear regression.

The models used in our analysis are subject to two potential problems. The first is an error in variables problem; measurement error exists in the independent variables (catch and effort) as well as the dependent variable (catch) used in the regression analysis. Errors in measurement of independent variables can lead to biased and misleading parameter estimates (Walters and Ludwig 1981).

The models we used are autoregressive because catch is predicted using the catch from previous years. This leads to the second potential problem: residuals that are not independent. Correlation among residuals may occur because catch and effort data for a single year are used to predict catch in other years. For example, in our analysis with model <111>, Walters' mod-

ification for incomplete recruitment and $k = 5$, we predict the catch in year t and then use the observed catch in year t to predict catch in years $t + 1$, $t + 2$, $t + 4$, $t + 5$, and $t + 6$. Correlations among residuals are likely because the error (residual) in catch for year t contributes to the residuals for five other years. Walters (1985) discussed bias in parameter estimation that results from lack of independence among residuals in time series analysis.

We used three methods to deal with these problems. The first method assumes that all variation in catch is "process error" (due to variation in biological characteristics of the stock and efficiency of the fisherman). Measurement errors are assumed to be unimportant or nonexistant. This is done by including a single error term in the model as in simple linear regression. Deriso (1980) used this approach with some success.

The second approach is to assume that all of the variation in catch is measurement error. Parameters are then estimated by "deterministic simulation," that is by substituting predicted catches from the model for the actual catches in the regression equation. Predicted catches, rather than the recorded catches, are used because predicted catch is assumed to be a more reliable estimate of the true catch. This procedure has also worked well in some cases (Deriso 1985; C. J. Walters, Institute of Animal Resource Ecology, University of British Columbia, 2075 Westbrook Place, Vancouver, B.C. V6T 1W5, pers. comm.). A problem with this approach is that predicted values for catch are not available for the first $k + 1$ years of data. One could treat the first $k + 1$ catches as parameters and attempt to estimate them by nonlinear regression but, in our experience, it is better to keep the number of such parameters to a minimum. Another possibility is to use a moving average (e.g. $C^*_2{}' = (C^*_1 + C^*_2 + C^*_3)/3$ where $C^*_2{}'$ is the moving average estimate of C^*_2). Because it was simpler, we used actual values for catch when predicted values were not available.

The third possibility, discussed by Schnute (1985), is to include two independent error terms in the model. The formulation for models with two error terms in our analysis was

$$\ln (C^*_{t+1}) = \ln (M\{X_{t+1},\theta\}) + \epsilon_{t+1} + \lambda\epsilon_t$$

where $M\{\ \}$ is the model, X_{t+1} is the vector of catch and effort data use to predict catch in year $t + 1$, θ is the parameter vector, ϵ_t is the residual for year t, and λ is an additional parameter (constrained so that $-1 < \lambda < 1$) that reflects the importance of ϵ_t in the prediction for time $t + 1$. A disadvantage of this approach is that two additional parameters (λ and ϵ_0) must be estimated. An advantage is that the model with a single error term is nested in the model with two error terms so that the necessity for the second error term can be evaluated by a likelihood ratio test.

Model Selection

We began our analysis by fitting the "full" model <111> to the data assuming all process error. The full model was modified, as described above, so that it reflected our perceptions about mortality and recruitment (i.e. natural mortality followed by a pulse of fishing mortality, Beverton and Holt recruitment curve, and recruitment to the gear during ages IV and V). Second, we fitted the smaller, knife-edge version of <111> in order to determine if the parameters for incomplete recruitment were justified. This was done by setting one of π_{k-1} and π_k equal to zero and the other equal to 1. If the full model was significantly better than the knife-edge model by a likelihood ratio test, then the full model was used. If the full model was not significantly better, then the knife-edge version was adopted.

The next step in selecting a model was to test the appropriate version of model <111> against the smaller, constant recruitment model <114>. This was done by setting the parameter δ in the Beverton–Holt recruitment curve equal to zero. If <114> fitted the data as well as the larger model <111>, then the constant recruitment model <114> was adopted. Model <114> does not include lags of k and $k + 1$ years for recruitment so that there are more years of data available for parameter estimation with model <114> than with <111>. In order to make comparisons valid, we fitted model <114> initially using the same set of data that was used to fit <111>. If <114> was preferable, then we fitted it using all of the available data.

After a model was selected (the full model, knife-edge version or constant recruitment version), we concentrated on determining which error structure was most appropriate. The first step in this process was to fit a model with two independent error terms. The larger model with two error terms was adopted if it fitted the data significantly better than the smaller model with a single error term; otherwise, the smaller model was retained.

Finally, we fitted the best model by deterministic simulation (assuming all measurement error). A likelihood ratio test cannot be used to choose between the assumptions of all process and all measurement error because the models are not nested. We simply adopted the assumption and model that gave the most reasonable parameter estimates. If there was no clear reason to prefer one or the other, then we chose the model with all process error because of its simplicity.

Some additional criteria were used to evaluate the suitability of models. We plotted standardized residuals against time as well as against predicted catch in order to determine if residual variance changed as a function of either. We adopted models that exhibited no pathological patterns in the residual plots. A runs test (Sokal and Rohlf 1981) was used to test the null hypothesis ($\alpha = 0.05$) of no serial correlation in the residuals. Models with serially correlated residuals were rejected.

Likelihood Ratio Test For Nested Models

Sets of nested models were evaluated by likelihood ratio tests (Lindgren 1976, p. 307–309). Consider two models in a nested set: a large model with j parameters and a smaller submodel with q parameters ($j > q$). The large model will always explain more of the total variation in the data than the small model because of the extra parameters. The question is whether the additional variation explained is sufficient to justify the extra parameters. The following is a test statistic that can be used to determine if the large model explains significantly more of the total variation than the small model:

$$\Lambda = n \ln (\mathrm{RSS}_S/\mathrm{RSS}_L)$$

where RSS_S denotes the residual sum of squares for the small model, RSS_L denotes the residual sum of squares for the large model, and n is the number of observations. When n is large and the residuals are normally distributed the test statistic (Λ) has a chi-square distribution with $j - q$ degrees of freedom. We rejected the null hypothesis when the probability value for a test was less than or equal to 0.05.

Our approach to model selection was not completely objective. The models that we used reflected our prior notions about the fishery and biology of lake herring. The order in which we fitted alternative models (alternative error structures last) may

have affected our results. This situation is analogous to various "stepwise" procedures for identifying the best model in multiple linear regression; the model finally chosen may depend on the order in which variables were added to or deleted from the model. In defence of our approach it can be said that (1) we were able to deal effectively with a large number of possible models, (2) the use of likelihood ratio tests for nested models made our analysis more objective than it would have otherwise been, and (3) our assumptions about underlying biological processes were clearly stated.

Results

The constant recruitment model <114> with a single error term and all process error was the most satisfactory model for the lake herring fisheries in Black Bay and Thunder Bay. It is worth noting, however, that the likelihood ratio test for the necessity of including two error terms in model <114> was almost significant ($p = 0.06$) in the case of both Black Bay and Thunder Bay. Regressions involving <111> were ill-conditioned and parameter estimates were difficult to obtain. There was an obvious pattern in the recruitment curves for model <111>; predicted recruitment was nearly constant over a wide range of stock biomass. Apparently, the regression procedure found no evidence of a relationship between spawning stock biomass and recruitment in the data for either Black Bay or Thunder Bay lake herring. This result suggested that the parameters used to describe recruitment in model <111> were either unnecessary or not estimable from the available data. We were not surprised, therefore, when the likelihood ratio tests indicated that the constant recruitment model <114> was preferable. The version of model <114> with all measurement error was rejected because the estimates of M obtained by deterministic simulation were more unreasonable than those obtained using all process error.

Parameters for model <114> with process error structure were relatively easy to estimate. The regression routine converged quickly and solutions appeared to be global (judging by repeated trials with different initial values for parameters). No pathological problems were apparent in residual plots for model <114> with process error structure. There was no evidence of serial correlation among residuals (approximate probability values from the runs test were 0.33 for Black Bay and 0.63 for Thunder Bay).

The final model (<114> with all process error) explained 77% of the total (log-transformed) variation in catch for Black Bay lake herring and 65% of total variation for Thunder Bay lake herring. Parameter estimates and regression statistics for Black Bay and Thunder Bay lake herring are given for all models in Table 5. Approximate correlations among parameter estimates for the final model are given in Table 6.

Discussion

Predicted Values For Catch

Figures 1 and 2 show the observed and predicted values for catch obtained from model <114> with all process error. Predicted values are "one step ahead" predictions obtained using the final parameter estimates. Roff (1983) pointed out that predicted values from Deriso's (1980, fig. 3) analysis consistently lag behind the observed values by 1 yr. It is interesting to note that such lags are not evident in the plots for Black Bay and Thunder Bay.

Parameter Values

Estimates for the rates of natural mortality (M) and recruitment (R_m) in model <114> were poor. The estimates of M for Black Bay and Thunder Bay (2.27 and 1.33, respectively) are certainly too high, since these instantaneous rates correspond to annual survival rates of 0.10 and 0.26 in the absence of fishing. Correlations between estimates of M and R_m for both Black Bay and Thunder Bay were nearly unity. We can safely assume, therefore, that the estimates of R_m are too large as well. The mutual uncertainty in these parameters could be resolved if there was an external estimate of one of them. This point reemphasizes the problem with using catch and effort data to estimate both M and R_m in model <114> as well as the need for reliable external estimates of either M or R_m.

Estimates of catchability coefficients (q) were not highly correlated with estimates of other parameters and were probably more reliable. The estimate of q for Black Bay (0.47) was greater than that for Thunder Bay (0.13), suggesting that small-mesh gill nets set in Black Bay during November are 3.6 times more efficient than nets set in Thunder Bay during December.

Plausibility of Models

How reasonable, in biological terms, is the assumption of no relationship between spawning stock size and recruitment in model <114>? Lake herring fisheries in Thunder Bay and Black Bay have persisted despite intensive exploitation; recruitment has, so far, been adequate to maintain the stocks. The collapse of other Lake Superior lake herring fisheries due to recruitment failure following overexploitation is, however, well documented (Selgeby 1982). It is possible that effects of spawning stock biomass on recruitment were negligible over the range of stock densities observed during this study, but it is also possible that such effects were obscured by environmental variation and measurement error (Walters and Ludwig 1981). The important conclusion is that the factors affecting recruitment of Black Bay and Thunder Bay lake herring remain unknown.

Abundance of Lake Herring

Estimates of abundance can be obtained from eq. 2.5 in Schnute (1985) as the "catch-per-unit-mortality":

$$N^*_t = C^*_t/(1 - \phi_t).$$

Abundance of lake herring in Thunder Bay during 1948–79 and Black Bay during 1951–79 was estimated from the catch and effort data using the estimated values for q and a value of 0.4 for M (Selgeby 1982). The trends in estimated abundance (Fig. 1 and 2) are similar to those in CPUE.

Abundance of lake herring in Black Bay appears to have fluctuated widely but with no particular trend. No relationship between effective fishing effort and abundance is apparent despite the high effective effort for Black Bay during 1968–70 and a general trend of increasing effective effort since 1951. This observation may reflect an insensitivity of the fishery to fishing at the effort levels employed during 1951–79. Alternatively, the observation may reflect the relatively constant levels (with the exception of 1968–70) of effective fishing effort in Black Bay during the study period.

Abundance of lake herring in Thunder Bay appears to have been intermediate prior to 1956, high during 1956–64, low during 1965–71, intermediate during 1972–79, and to have fluctuated widely throughout the study period. High fishing

TABLE 5. Parameter estimates and summary statistics for all models fit to the Black Bay and Thunder Bay lak
of squares, Λ is the likelihood ratio test statistic, and SS is the total sum of squares for the dependent variable
indicates that a parameter or summary statistic is not applicable to a particular model. Likelihood ratio tests
other "small") as described in the text. The small model in a test is the model on the same line as the test statis
value of the test statistic as large or larger than the value given under the null hypothesis that the small mod

Model	Parameters estimated from auxiliary data				Pa by r		
	k	ρ	V	v	q	M	R_m
Black Bay							
Set 1 (N = 23, SS = 1.96)							
⟨111⟩ with incomplete recruitment	5	1.0	1.55×10^{-6}	1.04×10^{-6}	0.763	0.994	$1.38 \times 10^{}$
⟨111⟩ with knife-edge recruitment	5	1.0	1.55×10^{-6}	1.04×10^{-6}	0.760	1.00	$1.38 \times 10^{}$
⟨114⟩ with one error term	—	1.0	1.55×10^{-6}	1.04×10^{-6}	0.722	0.909	$9.31 \times 10^{}$
Set 2 (N = 27, SS = 10.8)							
⟨114⟩ with two error terms	—	1.0	1.55×10^{-6}	1.04×10^{-6}	0.590	3.56	$1.44 \times 10^{}$
⟨114⟩ with one error term	—	1.0	1.55×10^{-6}	1.04×10^{-6}	0.467	2.27	$4.21 \times 10^{}$
⟨114⟩ by deterministic simulation	—	1.0	1.55×10^{-6}	1.04×10^{-6}	0.570	4.24	$2.79 \times 10^{}$
Thunder Bay							
Set 1 (N = 26, SS = 11.78)							
⟨111⟩ with incomplete recruitment	5	1.0	1.55×10^{-6}	1.04×10^{-6}	0.174	1.25	$1.76 \times 10^{}$
⟨111⟩ with knife-edge recruitment	Not applied to the data for Thunder Bay lake herring be						
⟨114⟩ with one error term	5	1.0	1.55×10^{-6}	1.04×10^{-6}	0.117	1.34	$2.22 \times 10^{}$
Set 2 (N = 30, SS = 12.21)							
⟨114⟩ with two error terms	—	1.0	1.55×10^{-6}	1.04×10^{-6}	0.00444	0.461	$9.80 \times 10^{}$
⟨114⟩ with one error term	—	1.0	1.55×10^{-6}	1.04×10^{-6}	0.132	1.33	$2.00 \times 10^{}$
⟨114⟩ by deterministic simulation	—	1.0	1.55×10^{-6}	1.04×10^{-6}	0.116	3.04	$1.63 \times 10^{}$

er Bay lake herring data. N is the number of observations used for parameter estimation, RSS is the residual sum
nt variable (ln catch) in the regression analyses; all other symbols and parameters are defined in Table 1. A dash
ratio tests were used to select the most appropriate model from a pair of nested models (one called "large," the
test statistic (Λ); the large model is on a line above the small model. The p-value is the probability of obtaining a
mall model is adequate. Solutions that may not be global are indicated in the column labeled "Comment."

Parameters estimated by nonlinear regression						Summary statistics					
R_m	δ	π_4	π_5	λ	ϵ_0	df	RSS	R^2	Λ	p-value	Comment
38×10^7	3.96	0.0256	0.974	—	—	18	1.17	40%	—	—	
38×10^7	3.89	—	1.00	—	—	19	1.17	40%	0.00	1.00	
31×10^6	—	—	—	—	—	20	1.31	33%	2.60	0.11	Best of set
44×10^8	—	—	—	0.373	−1.71	22	2.05	81%	—	—	
21×10^7	—	—	—	—	—	24	2.52	77%	5.57	0.06	Best overall
79×10^8	—	—	—	—	—	—	2.64	76%	—	—	Global?
76×10^7	6.45	1.0	0.0	—	—	21	4.12	65%	—	—	
erring because the parameter estimates for the model above give knife-edge recruitment											
22×10^7	—	—	—	—	—	23	4.20	64%	0.500	0.78	Best of set
80×10^7	—	—	—	−1.00	−0.153	25	3.54	71%	—	—	Global?
00×10^7	—	—	—	—	—	27	4.25	65%	5.48	0.06	Best overall
63×10^8	—	—	—	—	—	—	5.35	56%	—	—	

TABLE 6. Approximate correlations among the final parameter estimates for model <114>. M is the instantaneous rate of natural mortality, q is the catchability coefficient, and R_m is the number of age V fish recruited annually.

	Black Bay		Thunder Bay	
	M	q	M	q
q	0.07		0.21	
R_m	1.00	0.00	0.98	0.00

efforts during 1948–52 may account for declining abundance during the same period. Low levels of effective fishing effort beginning in 1970 are associated with partial recovery of the stock and intermediate levels of abundance that begin in 1972. These observations suggest that fishing effort, at the levels observed in this study, can affect abundance of lake herring in Thunder Bay.

Management Implications

Our analysis suggests that recruitment to the Thunder Bay and Black Bay stocks is independent of escapement over the range of escapement levels observed during this study. This hypothesis is a tentative one, since there are obvious limitations in the data and our analysis.

The apparent independence between escapement of lake herring and recruitment to the Black Bay and Thunder Bay fisheries leads us to suggest that an $F_{0.1}$ management policy based on a yield-per-recruit model (Ricker 1975; Deriso 1987) might be effective for management of these fisheries. Another management scheme would take advantage of periods of high abundance while providing some protection to the stocks during periods of low abundance. This would only be possible if abundance of lake herring could be determined early in the fishing season and quotas could be implemented effectively as the season progressed.

Conclusion

Schnute's (1985) models and approach to modeling appear useful for analysis and management of Lake Superior lake herring stocks. There is, however, an unresolved problem with estimation of the parameters for natural mortality (M) and recruitment (R_m) in the constant recruitment model <114>. Success in using these models seems to depend, in large measure, on the choice of an appropriate and parsimonious version of the basic model and on the availability of auxiliary information about growth, recruitment, and mortality.

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Economic Analysis of Fishery Rehabilitation Under Biological Uncertainty: A Conceptual Framework and Application

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Using the commercial yellow perch (*Perca flavescens*) fishery of Green Bay, Lake Michigan, as an example, we outline a conceptual framework for estimating economic gains from fishery rehabilitation in the presence of biological uncertainty. Three steps underlie the framework: (a) identifying the key biological uncertainties which hamper forecasts of stock changes induced by rehabilitation efforts; (b) developing plausible "future biotic states" that encompass these uncertainties and their probabilities of occurrence; and (c) estimating the "expected value" of economic gains for commercial fishers from an ongoing rehabilitation plan across these future biotic states. Using this approach, the expected economic gains for commercial fishers from rehabilitation are found to be roughly zero for most plausible scenarios. Since sport gains under this rehabilitation plan are probably substantial, and other economic impacts (regulatory costs and final consumer effects) appear to be small, the analysis suggests that the overall economic gains from the plan are positive.

En prenant comme exemple la pêche commerciale de la perchaude (*Perca flavescens*) à Green Bay au lac Michigan, nous présentons une approche pratique pour évaluer les avantages économiques du rétablissement de la péche malgré l'incertitude biologique. Trois étapes sont à la base de cette approche : (a) identifier les principales incertitudes biologiques qui entravent les prévisions de changements dans les stocks provoqués par les efforts de rétablissement; (b) concevoir des "états biotiques futurs" vraisemblables qui englobent ces incertitudes et leurs probabilités d'apparition; et (c) estimer la "valeur escomptée" des avantages économiques par les pêcheurs commerciaux à partir d'un plan permanent de rétablissement passant par ces états biotiques futurs. En utilisant cette approche, les avantages économiques escomptés pour les pêcheurs commerciaux, suite au rétablissement, s'avèrent être à peu près nuls pour la plupart des scénarios vraisemblables. Vue que les gains du point de vue sportif dans le cadre de ce plan de rétablissemant sont probablement substantiels et que d'autres répercussions économiques (frais de réglementation et effets définitifs sur les consommateurs) semblent être faibles, l'analyse porte à croire que les avantages économiques globaux découlant du plan sont positifs.

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Near-term harvest restrictions form a vital part of most fishery rehabilitation plans. As a result, affected user groups may initially experience lower economic returns. These losses may be recouped from eventual harvest gains induced by rehabilitation, but the size, timing, and duration of these gains are often uncertain due to the presence of key biological unknowns. Most rehabilitation plans, then, are risky undertakings, in which near-term, certain costs are incurred in order to obtain far-term, uncertain benefits. From an economic viewpoint, rehabilitation is a risky "investment" in a fishery biomass, the latter being regarded as a form of "biological capital" which can sustain a flow of harvests over time (Clark and Munro 1975). The primary "investors" (and thus the risk bearers) are the affected user groups who must forego near-term harvests.

Under these conditions, how can managers assess the economic consequences of rehabilitation efforts? We address this question by estimating economic gains for commercial fishers from a rehabilitation plan which was initiated in 1983 by the Wisconsin Department of Natural Resources (WDNR) for the yellow perch (*Perca flavescens*) fishery in the Wisconsin

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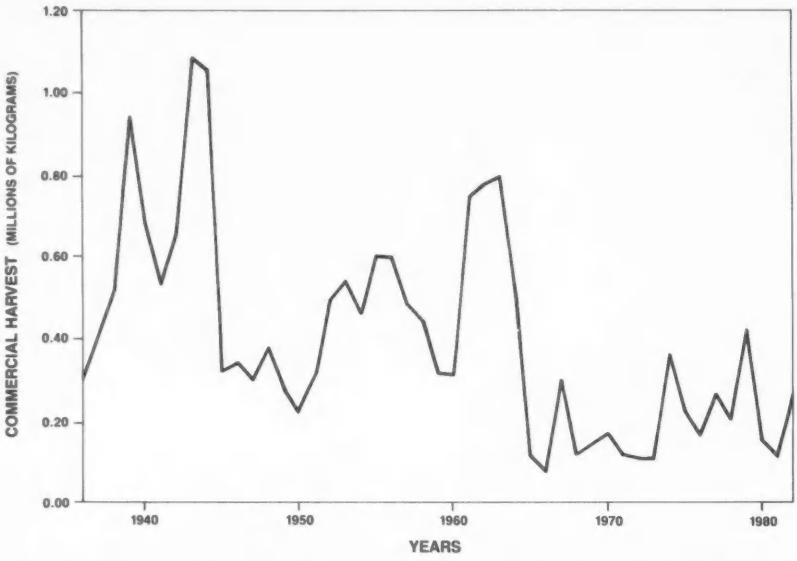

FIG. 1. Annual commercial harvests of yellow perch from the Wisconsin waters of Green Bay, Lake Michigan, 1936–82.

waters of Green Bay, Lake Michigan. Our conceptual framework, which is drawn in part from ideas in Walters (1986), involves (a) identifying the key biotic uncertainties of this fishery which hamper predictions of stock changes induced by rehabilitation efforts, (b) constructing plausible "future biotic states" that encompass the uncertainties and their probabilities of occurrence, and (c) relative to an alternative "baseline" policy, estimating the "expected value" of economic gains for commercial fishers under the WDNR rehabilitation policy across these biotic states. In carrying out these steps, our primary goal is to outline a practical approach for integrating biological uncertainty into an economic analysis of an actual fishery rehabilitation program.

Our major empirical focus is on commercial fishing impacts induced by the 1983 WDNR plan, for prior to 1983 this user group caught approximately 85% of the total Green Bay perch harvest (WDNR 1982). Commercial catch restrictions also form the heart of the WDNR plan (WDNR 1986). Thus, Green Bay commercial fishers are the major risk bearers of this policy change. However, the economic well being of Green Bay sport anglers is also being modified by the rehabilitation policy. (In contrast, final perch consumers are unlikely to be greatly affected, for Green Bay dockside prices are highly insensitive to Green Bay catch levels (Milliman 1985).) Detailed data on the sport fishing impacts are not yet available, but their general magnitude can be roughly estimated. Regulatory cost estimates associated with the WDNR rehabilitation policy are also available. These data, when combined with our commercial fishing results, will allow us to tentatively assess the overall economic gains induced by the Green Bay rehabilitation plan.

Overview of the Green Bay Yellow Perch Fishery and the Key Biotic Uncertainties

Green Bay has historically supported an active commercial yellow perch fishery, with gill nets and drop nets (a type of fyke net) each supplying roughly half of the commercial catch in recent years (Kraft 1982). In 1965 the fishery suffered a partial harvest collapse. While commercial catches averaged 525 000 kg annually from 1936 to 1964, the 1965–82 annual harvest average has been approximately 204 000 kg (Fig. 1). Possible reasons for the 1965 collapse include commercial overfishing, pollution, and an increase in alewife (*Alosa pseudoharengus*) abundance (Kraft 1982). Prior to 1983, the major commercial fishing regulations were a closed season during spawning (April 9 – May 20) and a minimum commercial legal size limit of 191 mm. These regulations constitute the baseline policy of the analysis.

In 1983 the WDNR initiated several new regulations with the primary goal of rehabilitation (WDNR 1982): (a) a total limit on commercial catch, adjusted annually, which in turn is divided up into individual, transferable catch quotas, and (b) an expanded closed season for drop nets during late May and June in order to reduce the mortality of sublegal perch (fish below 191 mm) which often die in drop nets during this time period. These new restrictions, plus the pre-1983 regulations, constitute the rehabilitation policy of the analysis.

With rehabilitation, the WDNR hopes to attain the harvest goals listed in Table 1 by 1991 (WDNR 1986). Relative to the recent historical average, combined commercial and sport harvests are to increase by between 48 and 91%. In addition, catch-per-unit-of-effort (CPUE) levels are expected to increase for gill nets and drop nets.

How the Rehabilitation Policy is to Work

The WDNR expects the rehabilitation policy to work as follows (WDNR 1986):

> Initiation of a quota-controlled fishery to allow development of a more normal age structure will produce an increased average weight-per-fish-harvested (increased yield per recruit). This quota system, combined with reduced mortality [from drop nets] ... and a more stable spawning population, will allow maintenance of a more abundant population.

TABLE 1. Wisconsin Department of Natural Resources 1991 harvest goals and the recent annual historical harvest averages for the Green Bay, Wisconsin, yellow perch fishery.

	1991 goals (kg)	Recent historical averages (kg)[a]
Commercial fishery		
Catch	272 200[b]	217 300[d]
Dropnet CPUE	11.8[c]	9.0[d]
Gillnet CPUE	17.7[c]	8.6[d]
Sport fishery		
Catch	108 900–215 500[b]	38 600[d]
Total catch	381 100–487 700	255 900

[a]Future dockside prices are expected to be high, and commercial fishers appear to fish harder with high prices (Milliman 1985). Thus, to preserve comparability with the 1991 harvest goals, the recent historical catch and CPUE averages are derived from the 10 post-1964 years (1973, 1975–79, 1981–84) which had high dockside prices (above $0.45/kg in 1983 U.S. dollars). The 1983 and 1984 harvest figures which entered into these calculations are WDNR estimates of what harvests would have been in the absence of the 1983 rehabilitation plan (B. Belonger, WDNR, Box 16, Industrial Parkway, Marinette, Wisconsin, 54143, USA, pers. comm.).

[b]WDNR (1986).

[c]B. Belonger (pers. comm.).

[d]WDNR (1982) and unpublished data from B. Belonger (pers. comm.).

The WDNR has also supplied the following additional information on the Green Bay perch population (WDNR 1982):

> The southern Green Bay perch population consists largely of young fish. These young fish are "inefficient" spawners compared to older perch. For example, a 7 1/2 inch [191 mm] female perch will deposit an average of 15,400 eggs in a spawning season, while an older, 13 1/2 inch [343 mm] perch will deposit an average of 104,000 eggs. In southern Green Bay at present, the spawning success in any year depends on the egg production of these young fish and the unpredictable effects of the weather ...
>
> In 1977, for instance, warming conditions [were favorable] and the number of fish spawning was high. Thus a strong 1977 "year class" of perch was produced.

Thus, by reducing the mortality of juvenile and young adult perch, the harvest restrictions will induce rehabilitation by (a) enhancing the yield per recruit and (b) increasing the number of recruits to the fishery via a positive stock–recruitment relationship and lesser mortality of sublegal perch in drop nets.

Key Biological Uncertainties

Two knowledgeable biologists (B. Johnson, co-author, and B. Belonger, WDNR, Box 16, Industrial Parkway, Marinette, WI 54143, USA, pers. comm.) have identified the following biotic uncertainties which hamper predictions of stock changes induced by rehabilitation efforts.

(1) Will growth rates drop as the perch population expands, thus retarding yield-per-recruit increases?

(2) Does a positive, significant stock–recruitment relationship exist at current and higher abundance levels?

(3) Will future alewife abundance levels in the Bay remain high? Alewife abundance is declining in Lake Michigan proper (Jude and Tesar 1985), but it is not yet known whether this decline will spread to Green Bay (D. Steward, Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706, USA, pers. comm.). Reduced local alewife stocks may enhance perch abundance under both policies (baseline and rehabilitation).

While the above uncertainties influence the extent of eventual stock response due to rehabilitation efforts, the speed of stock response is determined in part by variability in random factors such as spring weather conditions, which can have a marked impact on spawning success (B. Belonger, pers. comm.). Favorable random factors at the beginning of rehabilitation efforts may greatly speed stock response by producing one or more large year-classes; unfavorable near-term random factors may have the opposite effect.

Future Biotic States and Their Associated Probabilities of Occurrence

Future biotic states were initially broken into two broad categories: states with high alewife abundance levels (which mirror the recent historical past) and states with low alewife abundance levels. Unfortunately, the analysis cannot credibly encompass the latter category, for the 1991 WDNR harvest goals listed in Table 1 were originally constructed in 1983, when alewife declines in Lake Michigan proper (and thus possibly Green Bay) had not yet been documented. Thus, the analysis is applicable only to states in the high alewife abundance category. We list these latter states below, together with a qualitative description of the extent and speed to which perch abundance might plausibly increase due to rehabilitation efforts.

(1) *The Optimistic States*: Growth is not strongly density dependent, and a significant, positive stock–recruitment relationship exists. Perch abundance increases greatly under the rehabilitation policy; eventual harvests are near the 1991 WDNR harvest goals. Two optimistic states exist: an "optimistic–fast" state, in which recruitment and yield-per-recruit increase quickly under rehabilitation due to favorable near-term random factors (such as good spring weather), and an "optimistic–slow" state, in which these increases occur more slowly due to poor near-term random factors.

(2) *The Moderate States*: Growth is somewhat density dependent, and/or a positive stock–recruitment relationship is slight or nonexistent. A smaller but still significant increase in perch abundance occurs under the rehabilitation policy; eventual harvests fall somewhere between the 1991 WDNR harvest goals and the baseline policy harvests. As with the optimistic group, two moderate states exist, a "moderate-fast" state and a "moderate–slow" state, which represent fast and slow stock responses, respectively, due to favorable or unfavorable near-term random factors.

(3) *The Pessimistic States*: Growth is strongly (and negatively) density dependent, and a positive stock-recruitment relationship does not exist at current abundance levels. At best, a slight increase in perch abundance occurs under the rehabilitation policy; eventual catches remain near the baseline levels, although the harvest split between sport and commercial user groups may change. Two pessimistic states exist which are politically as well as biologically determined: a "pessimistic–sport favored" state, in which the WDNR permanently restricts commercial catch so as to increase sport catch, and a "pessimistic–commercial favored" state, in which the WDNR rehabilitation plan is eventually abandoned and replaced with the baseline policy.

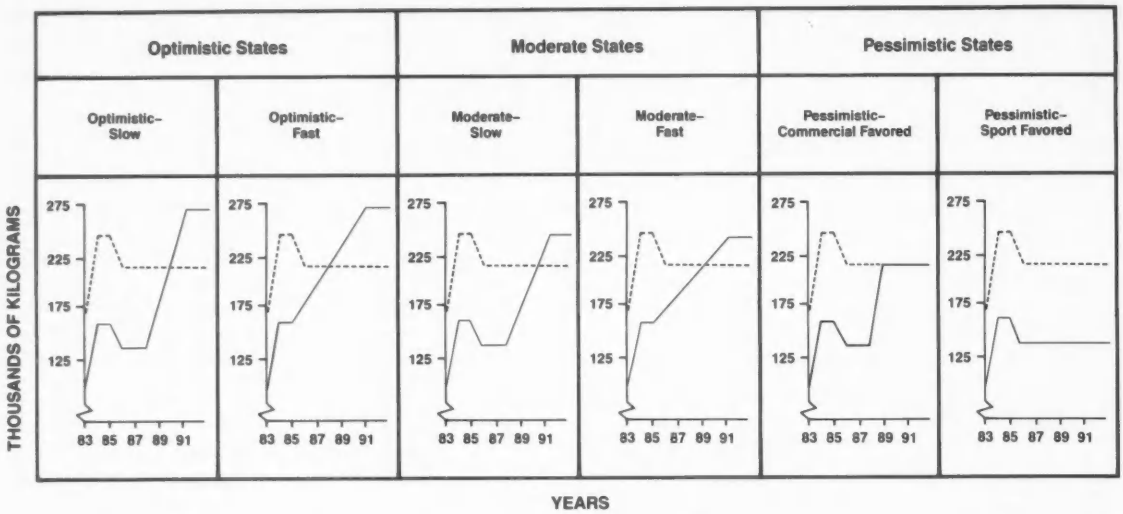

FIG. 2. Harvest time paths under the rehabilitation (—) and baseline (- - -) policies for all future biotic states and harvest time paths with high alewife abundance.

Assigning Probability Ranges to Future Biotic States

Probability ranges are initially assigned to future states based on the extent of eventual stock response due to rehabilitation efforts (the optimistic, moderate, and pessimistic groupings). Separate estimates were obtained from two biologists (B. Johnson, co-author, and B. Belonger, pers. comm.). Their estimates were similar and were merged into a single composite set by forming ranges which encompassed the individual range estimates (thus, one source assigned odds of 0.40–0.80 to the optimistic states, while the other assigned odds of 0.60–0.80; the composite range is then 0.40–0.80). The composite set is listed below, together with the approximate range midpoints:

	Optimistic states	Moderate states	Pessimistic states
Probability ranges	0.40–0.80	0.10–0.50	0.00–0.15
Approximate range midpoints	0.60	0.30	0.10

While probability estimates based on the extent of eventual stock response under rehabilitation are available, similar figures for the speed of stock response (which is greatly influenced by weather and other random factors) are unavailable. Lacking dependable estimates, 50-50 conditional odds are assigned to the "fast" and "slow" states within the optimistic and moderate groups. A lack of information led to similar conditional odds being assigned to the "sport favored" and "commercial favored" pessimistic states.

The probability ranges for all six future biotic states are (0.5 × 0.4) to (0.5 × 0.8) for the optimistic–fast and optimistic–slow states, (0.5 × 0.1) to (0.5 × 0.5) for the moderate–fast and moderate–slow states, and (0.5 × 0.0) to (0.5 × 0.15) for the pessimistic–sport favored and pessimistic–commercial favored states.

Constructing Harvest and CPUE Time Paths

Drawing upon the 1991 WDNR harvest goals and the recent historical catch averages listed in Table 1, plausible harvest time paths for each future state–policy combination were constructed (Appendix). These time paths are input data into the economic measures of commercial fishing gains induced by rehabilitation. Rehabilitation and baseline harvests for the years 1983–85 have already been set or estimated (B. Belonger, pers. comm.), save for the 1985 baseline catch, which was estimated separately by Milliman (1985). These catches are as follows:

Year	Rehabilitation catch (kg)	Baseline catch (kg)
1983	90 700	158 600
1984	158 800	242 200
1985	158 800	242 200

Beyond 1985, catches under the rehabilitation policy are assumed (Fig. 2) to (a) rise to 272 200 kg in 1991 (the WDNR commercial catch goal) and then remain there under the optimistic states, (b) rise to 244 500 kg in 1991 (half way between WDNR 1991 catch goal and the recent historical catch average of 217 300 kg) and then remain there under the moderate states, and (c) remain at 136 000 kg forever (the 1983–85 rehabilitation catch average) under the pessimistic–sport favored state, but revert to 217 300 kg in 1988 under the pessimistic–commercial favored state (when the rehabilitation policy is replaced by the baseline policy). Catches under the optimistic–fast and moderate–fast states begin rising linearly to their respective 1991 levels in 1986, while the optimistic–slow and moderate–slow states equal 136 100 kg in 1986 and 1987, and then begin rising linearly to their respective 1991 levels in 1988. Actual rehabilitation harvests are, of course, expected to fluctuate but are assumed to approximately correspond on average to one of the harvest time paths outlined above.

Annual baseline policy harvests are assumed to equal the recent historical catch average of 217 300 kg beyond 1985 for all six states.

Also associated with each future state–policy combination are specific time paths for gillnet and dropnet CPUE levels

(Appendix). The CPUE time paths are constructed in a manner similar to the harvest time paths, with CPUEs (a) rising linearly to the WDNR CPUE goals by 1991 under the optimistic states, (b) rising linearly to levels half way between the WDNR CPUE goals and the recent historical CPUE averages by 1991 under the moderate states, and (c) remaining at the recent historical CPUE averages under the pessimistic states. CPUE increases begin 2 yr earlier than harvest increases on the premise that perch abundance (and thus CPUEs) will increase before harvests are allowed to rise.

Commercial Fishing Economic Results

Calculating Economic Gains for Commercial Fishers: Overall Approach

Our economic methodology is described in detail in Milliman (1985). We outline it briefly here. Using standard benefit-cost tools and the harvest and CPUE time paths described above, commercial fishing economic gains ("producer rents" in economic terminology) can be estimated for each future state–policy combination. Producer rents in a given year are defined as annual fishing revenues minus annual variable fishing costs, with the latter including the wages that fishers could have earned from other jobs had they chosen not to fish.

Annual fishing revenues are estimated in the following manner. A price forecasting equation was estimated from annual 1958–82 data (t statistics in parentheses):

$$(1)\quad \log P = \underset{(-4.334)}{-13.8787} - \underset{(-5.227)}{0.202819}\cdot\log Q^{WI} - \underset{(2.640)}{0.653282} \times \log Q^{LE} + \underset{(1.575)}{0.331540}\cdot\log P^{O} + \underset{}{2.31165} \times \log \mathrm{POP},\ R^2 = 0.961$$

where P is the annual Green Bay dockside price in constant 1983 U.S. dollars, Q^{WI} is the annual Wisconsin yellow perch harvest (the Green Bay harvest plus fish from the Wisconsin waters of Lake Michigan proper), Q^{LE} is the remaining annual Great Lakes catch (of which Lake Erie is the primary source), P^{O} is the price of ocean perch (a restaurant substitute), and POP is the population of Wisconsin, where the majority of the North American perch catch is consumed. All variables have the expected signs and are significant at the 10% confidence level or better using one-tailed tests of expected signs. Future values for Q^{WI}, Q^{LE}, P^{O}, and POP are plugged into this equation to forecast prices, which are then multiplied by the predicted Green Bay total harvest (derived from relevant harvest time path) to arrive at estimates of total fishing revenues. Future projections of the independent variables as well as the rationale and estimation of equation (1) are covered at length in Milliman (1985).

Annual fishing costs are estimated by first dividing total catch for each gear type by its predicted CPUE level (obtained from the relevant CPUE time path) to yield an estimate of total fishing effort. For example, if gill netters for a given year, policy, and future biotic state are expected to catch 100 000 kg, and if their predicted CPUE is 10 kg, then total gillnet fishing effort is 10 000 units (100 000 divided by 10). Total fishing effort is then multiplied by the average cost per unit of effort to arrive at total effort costs. The average cost per unit of effort (including wages foregone due to fishing) was calculated from cost data collected via personal interviews with commercial fishers and are \$14.01 for gill nets and \$6.23 for drop nets (in 1983 U.S. dollars) (see Milliman 1985 for details). When estimating harvests for each gear, we assume that the recent historical division of catch between the two gears will continue unchanged into the future.

We now illustrate how the annual producer rent estimates obtained from the above calculations are used to estimate economic gains from rehabilitation for commercial fishers. Let estimated rents for given year, policy, and future biotic state be RENT_t^{ij}, with subscript t denoting the year (t = 0,1,2,..., where 0 is 1983, 1 is 1984, etc.), superscript i denoting the particular policy (r for rehabilitation, b for baseline), and superscript j denoting future biotic states (j = 1,2,..., 6; 1 and 2 for the fast and slow optimistic states, 3 and 4 for the fast and slow moderate states, and 5 and 6 for the sport favored and commercial favored pessimistic states). Total "present value" rents for a given policy i and future biotic state j are

$$\sum_{t=0}^{T} \frac{\mathrm{Rent}_t^{ij}}{(1+k)^t}$$

where T is the time horizon of the analysis, i.e T = 20 when the rehabilitation policy is to be evaluated over the period 1983 to 2003. The k parameter is called the discount rate, and we briefly discuss its rationale, which in turn will illuminate the meaning of the term "present value." The discount rate adjusts ("discounts") future economic gains so that they can be expressed in current dollar (present value) terms. This adjustment is necessary because future gains are worth less than current gains, for current gains can earn interest by being placed in (say) a bank account. For example, the present value of \$1.00 earned 1 yr from now is \$0.952 today with a 5% interest rate. That is, this same dollar can be obtained next year by placing \$0.952 in the bank today, which will equal \$1.00 (\$0.952 + \$0.048 in interest) 1 yr hence. Mathematically, this present value calculation is

$$\frac{\text{Future gain}}{(1+k)^t} = \frac{\$1.00}{(1+.05)^1} = \$0.952.$$

If the interest (discount) rate is 10%, then the present value of \$1.00 1 yr hence falls to \$0.909, i.e. higher discount rates lower the present value of future economic gains. In turn, public projects which offer far term gains (such as many fishery rehabilitations plans) become less attractive economically. Discount rates are usually in "real terms," i.e. they have been adjusted to eliminate the effects of general inflation, and so are not meant to be a correction factor for inflation.

Two basic schools of thought exist on how the discount rate should be set for public projects (Sugden and Williams 1978).

(1) Following the reasoning given immediately above, one school sets the discount rate equal to interest rates found in private capital markets. For the current analysis, this would mean examining the interest rates faced by Green Bay commercial fishers when they invest in their fishing businesses. After being adjusted to eliminate the effects of general inflation, such a rate was calculated to be 7.82% (Milliman 1985).

(2) The other view states that the discount rate should reflect "social time preferences" for current versus future income, i.e. the discount rate should be collectively determined by society as a whole. Private rates of interest are not expected to accurately reflect these social preferences. Unfortunately, this second view offers little concrete advice as to what the correct "social" rate might be. We adopt a moderate rate of 4% to reflect this second

view, in part because casual empiricism suggests that social time preference advocates usually favor low to moderate rates of discount. Like the 7.82% rate, this rate is in "real terms," i.e. it has been adjusted to eliminate the effects of inflation. Besides reflecting this second view, using a 4% rate will allow us to observe how sensitive our results are to changes in this parameter.

Returning to the issue of estimating commercial fishing gains from rehabilitation, the change in present value rents induced by the rehabilitation policy r relative to the baseline policy b for a given future biotic state j is

$$\sum_{t=0}^{T} \frac{\text{Rent}_t^{rj} - \text{Rent}_t^{bj}}{(1+k)^t}$$

where the baseline policy rents signify what the fishers would have earned in the absence of the rehabilitation policy. This term can be positive or negative. The expected value of the change in producer rents induced by rehabilitation relative to the baseline policy across all future biotic states is

$$\sum_{j=1}^{6} \sum_{t=0}^{T} \left[P^j \cdot \frac{\text{Rent}_t^{rj} - \text{Rent}_t^{bj}}{(1+k)^t} \right]$$

where P^j is the probability that future biotic state j will occur.

Expected Value Estimates

Results cover two groups of fishers which harvest 79% of the commercial catch: gill netters with gillnet tugs (35%) and drop netters with dropnet boats (44%). The remaining 21% of the fishery uses both gear types, but employs smaller boats with outboard motors. A lack of detailed cost data on small boats prevented their inclusion into the actual estimates, but their costs do appear to be roughly similar to fishers with the larger boats. Thus, the results presented here probably mirror the economic impact of the rehabilitation policy on small boat fishers as well. The life of the Green Bay rehabilitation policy beyond 1991 is not known, and so economic results are given in 1983 U.S. dollars for four plausible time horizons: 10, 15, 20, and 25 yr. Given the extreme biological and regulatory uncertainties associated with fishery resources, predictions extending beyond 25 yr would probably have little credibility.

Expected value estimates are initially calculated using the approximate range midpoints (0.6–0.3–0.1) of the optimistic–moderate–pessimistic future biotic state groupings. As noted previously, 50–50 conditional odds are assigned to each pair of states found within each grouping. For a 10-yr horizon (1983–93), expected present value rent changes due to rehabilitation are negative, ranging from −$143 000 to −$180 000 in 1983 U.S. dollars (Table 2). These losses appear to be slight, with rents falling 4–6% relative to total baseline rents. Rent changes become slightly positive for the 15-yr time horizon, with rents increasing 3–6% under rehabilitation relative to the total baseline rents. Larger increases occur for the 20- and 25-yr time horizons, but are never particularly large (largest increase 14%). As expected, rehabilitation gains are greatest with a 4% discount rate, but both discount rates yield similar results for all four time horizons.

Expected value estimates are next calculated when high odds are assigned to the optimitic states and low odds to the moderate and pessimistic states (0.8–0.15–0.05). Gains from rehabilitation increase slightly (Table 3). Losses for the 10-yr time horizon are −$66 000 to −$119 000 (compared with −$143 000 to −$180 000 when the approximate range midpoints of the optimistic–moderate–pessimistic groupings are used). Rent changes as a percentage of total baseline rents continue to remain within (plus or minus) 10% of total baseline rents for all 10- to 15-yr time horizon estimates, and increase slightly thereafter. Rent changes with the 4 and 7.82% discount rates are similar.

TABLE 2. Expected present value rent changes in 1983 U.S. dollars induced by the Green Bay yellow perch fishery rehabilitation plan when probability range midpoints of the optimistic–moderate–pessimistic future biotic state groupings are utilized (0.6–0.3–0.1). High future alewife abundance is assumed. Rent changes as a percentage of total baseline rents are listed in parentheses under each rent estimate.

	Time horizon (yr)			
Discount rates (%)	10	15	20	25
4.0	−$143 000 (−4%)	$300 000 (+6%)	$669 000 (+11%)	$1 016 000 (+14%)
7.82	−$180 000 (−6%)	$180 000 (+3%)	$318 000 (+7%)	$470 000 (+9%)

TABLE 3. Expected present value rent changes in 1983 U.S. dollars induced by the Green Bay yellow perch fishery rehabilitation plan when high odds are assigned to the optimistic future biotic states and low odds are assigned to the moderate and pessimistic future biotic states (0.8–0.15–0.05). High future alewife abundance is assumed. Rent changes as a percentage of total baseline rents are listed in parentheses under each rent estimate.

	Time horizon (yr)			
Discount rates (%)	10	15	20	25
4.0	−$66 000 (−2%)	$459 000 (+9%)	$903 000 (+14%)	$1 313 000 (+17%)
7.82	−$119 000 (−4%)	$221 000 (+6%)	$438 000 (+9%)	$651 000 (+12%)

Finally, results are estimated with low odds for the optimistic states and high odds for the moderate and pessimistic states (0.4–0.45–0.15). Relative to figures based on the approximate range midpoints (Table 2), rehabilitation gains fall slightly (Table 4). However, all rent changes for the 10- and 15-yr time horizons again remain within (plus or minus) 10% of total baseline rents, and the use of different discount rates (4 vs. 7.82%) does not yield significantly different results.

Overall, the results are remarkably robust across different discount rates, probability sets, and time horizons. For the 10- and 15-yr time horizons, all rent change estimates are equal to (plus or minus) 10% of total baseline rents. The majority of rent change estimates for the 20- and 25-yr time horizons also fall within 10% of total baseline rents. Due to the biological and regulatory uncertainties inherent in fishery management, major emphasis should probably be placed on predictions for the 10- and 15-yr time horizons. In this case, commercial fishers appear to roughly break even under rehabilitation.

Additional Bioeconomic Factors Affecting the Rent Estimates

Since we are evaluating a complex policy change, a number of additional bioeconomic factors must be mentioned in order to

TABLE 4. Expected present value rent changes in 1983 U.S. dollars induced by the Green Bay yellow perch fishery rehabilitation plan when low odds are assigned to the optimistic future biotic states and high odds are assigned to the moderate and pessimistic future biotic states (0.4–0.45–0.15). High future alewife abundance is assumed. Rent changes as a percentage of total baseline rents are listed in parentheses under each rent estimate.

	Time horizon (yr)			
Discount rates (%)	10	15	20	25
4.0	−$220 000 (−6%)	$141 000 (+3%)	$436 000 (+7%)	$718 000 (+10%)
7.82	−$240 000 (−8%)	$6 000 (+0%)	$67 000 (+1%)	$288 000 (+5%)

properly assess the results. A summary is presented here with most details given in Milliman (1985). Additional factors which do not appear to greatly affect the analysis are variations in several important economic parameters, such as the division of catch between the two gear types, effort costs, or future Lake Erie harvest levels, the latter of which can have a marked impact on Green Bay dockside prices. Variations in these parameters often affect baseline and rehabilitation rents in a similar manner, and so the net difference in rents usually remains relatively unchanged. A fall in Green Bay alewife abundance may have a similar effect. Reduced local alewife stocks would probably increase harvest under both the baseline and rehabilitation policies. Hence, the net difference in rents between the two policies may not change greatly relative to the previous estimates.

A factor which may tend to increase economic gains from rehabilitation is the stabilization of harvests. However, at least some commercial fishers discount this possible benefit.

Several additional factors tend to lower economic gains from rehabilitation. Economic gains will fall if odds for the pessimistic states are larger than specified in this paper. Expected value calculations also do not take into account the possibility that people may wish to avoid situations where large-scale losses may occur, even if expected value calculations suggest that the possible benefits will exceed these losses on average. In economic terminology, such people are "risk averse." Commercial fishers probably perceive rehabilitation as the riskier policy, and so may rationally oppose this policy even though expected value calculations suggest that economic gains from rehabilitation are positive. It was not possible for us to adjust our results to take this phenomenon into account.

A factor which deserves special attention is catch underreporting, which could modify the results greatly. Catch underreporting probably occurred in this fishery prior to 1983, and might still be occurring now. Should economic gains from this nonreported catch be incorporated into the analysis? Thus far, only economic gains generated by reported catches have been counted. Credible arguments for and against counting gains from total catch (legal plus illegal) can be marshalled (Milliman 1986). If economic gains from total catch are counted, then the results of the analysis could be affected in the following manner. It is possible that catch underreporting was more common before 1983 than after (when the rehabilitation was initiated). This may be true because enforcement pressure increased in this fishery after 1983. This scenario suggests two points: (a) fishing revenue estimates based on reported catch may understate total revenues (and thus total economic rents) for both the baseline and rehabilitation policies and (b) relative to rehabilitation revenues, baseline policy revenues may be understated to a greater extent, for these latter revenues are derived from pre-1983 reported catches, when underreporting may have been more common. In turn, our analysis, which is based on reported catch only, could then overstate total (legal plus illegal) economic gains from rehabilitation relative to the baseline policy. Of course, if one believes that economic gains from only reported (legal) catch should be counted, then no overstatement is occurring.

The above differing impacts may cancel themselves out in the aggregate — but we cannot be sure. We regard our figures as "ballpark" calculations as opposed to precise estimates of producer rent changes.

Noncommercial Economic Effects of the Rehabilitation Policy

Final Consumer Impacts

The dockside demand curve facing this fishery is highly (although not totally) insensitive to the Green Bay yellow perch harvest level (Milliman 1985). Green Bay perch are eventually sold in a larger North American market which is dominated by Canadian Lake Erie harvests. From 1978 to 1982 the Green Bay yellow perch fishery supplied on average 3.3% of this larger market. Rehabilitation efforts would vary this figure by approximately 1.5% in either direction. Thus, we conclude that the economic well-being of final perch consumers is largely unaffected by the Green Bay rehabilitation plan.

Regulatory Costs

Regulatory costs due to the rehabilitation plan (biological monitoring and law enforcement expenses) equalled $70 241 in 1983 (Milliman 1985). These costs were not included in the producer rent change estimates presented earlier. To obtain a rough idea of their general magnitude across time, we assumed that the 1983 costs will continue unchanged into the future. For a 10-yr time horizon and a 7.82% discount rate, such costs in present value terms would equal $510 584 in 1983 U.S. dollars.

Sport Fishing Impacts

Unlike the commercial catches, Green Bay sport catches have not been significantly reduced under the rehabilitation policy, but will increase greatly if the 1991 WDNR harvest goals are totally or partially reached (see Table 1). Sport gains from the rehabilitation policy, then, are probably substantial under the optimistic states, and perhaps under the moderate states as well, and at worst are zero under the pessimistic states. To obtain a rough, lower bound estimate of sport fishing benefits generated by the WDNR rehabilitation plan, we carried out the following exercise. We start by noting that, from Table 1, attaining only half of the minimum projected sport harvest increase results in a 35 150 kg increase in sport catch ([108 900 −38 600 kg] / 2 = 35 150 kg). Such an increase is roughly equivalent to doubling the recent historical sport catch of 38 600 kg. In turn, doubling sport catch would probably increase the number of days fished by sport anglers. To explore the potential magnitude of sport fishing benefits induced by this enhancement, assume that the increase in fishing days is a modest 25%. We estimate that the recent historical sport catch of 38 600 kg has required roughly

91 768 angler fishing days annually (assuming that the catch per day equaled the 1982–83 WDNR creel census average of 5.9 fish, and that 14.027 fish equals 1 kg (B. Belonger, pers. comm.)). Thus, a 25% increase in days fished would equal 22 942 d. We further assume that such an increase occurs gradually over time, starting from zero in 1983 and increasing linearly to 22 942 d. in 1991. To arrive at an estimate of the economic benefits from this time path, we consulted Vaughan and Russell (1982), which is a detailed analysis of the national economic benefits generated by freshwater angling for the United States. This study recommends a range of $13.25–$29.41 (in 1983 U.S. dollars) when valuing additional angler days spent fishing for warmwater game fish or panfish. To be conservative, assume that the lower bound estimate of $13.25 is the value of an additional sport fishing day for Green Bay perch. The present value gains from the days fished time path are then $1 057 443 (in 1983 U.S. dollars) for a 10-yr time horizon and 7.82% discount rate. This estimate probably understates true sport fishing benefits for several reasons: (a) the increase in sport catch (and thus fishing days) may well be much larger; (b) the $13.25 figure used to value an additional sport fishing day is the minimal value recommended by the Vaughan and Russell study; and (c) this daily value figure ignores the possibility that rehabilitation may enhance the per day sport catch of perch, which in turn would probably increase the daily value of perch fishing.

Overall Economic Gains from the Green Bay Rehabilitation Plan

Drawing upon the biological and economic information cited above, it is possible to tentatively assess the overall economic gains from the Green Bay rehabilitation plan. As noted previously, commercial fishers appear to roughly break even under the WDNR rehabilitation plan, a result which is robust with respect to differing discount rates, future probabilities, and most time horizons. Final consumer impacts are also probably close to zero. Total economic gains from rehabilitation, then, are positive if the two remaining economic impacts generate positive economic gains, i.e. if sport benefits exceed regulatory costs. Our preliminary exploration of sport benefits and regulatory costs suggests that this will be the case: for a 10-yr time horizon and 7.82% discount rate, the present value sport benefits from a partially successful rehabilitation plan equal $1 057 443 under conservative assumptions, which is over twice the size of present value regulatory costs for the same time period ($510 584). Thus, combined economic gains (commercial plus consumer plus sport minus regulatory costs) from the WDNR plan appear to be positive. A more specific quantitative estimate of combined gains is not possible prior to the completion of research on sport fishing values, which is currently in progress.

In closing, we stress that our analysis is applicable only to the WDNR rehabilitation policy as originally implemented in 1983. Changes in this policy will affect the results. (However, the WDNR policy change which occurs with the pessimistic–commercial favored state is taken into account.) We also note that, unlike many previous bioeconomic analyses, we have not utilized a specific quantitative model, such as a Schaefer or Beverton–Holt model, to derive our harvest and CPUE time paths (Clark et al. 1973; Henderson and Tugwell 1979; Conrad and Adu-Asamoah 1986). Our major concern with utilizing these models in the analysis is that they are primarily intended to be analytical as opposed to prediction tools (Beddington et al. 1981). Since the prediction of economic impacts arising from an actual policy change is our major empirical objective, we have chosen to rely on biological data supplied by WDNR and academic biologists to construct harvest and CPUE time paths, as opposed to developing estimates from a fish population model with uncertain predictive powers. Many of our biological assumptions are drawn from an extensive, ongoing investigation of this fishery which was initiated by the WDNR in 1978 (WDNR 1982). Development of a detailed, quantitative Green Bay bioeconomic model with credible predictive powers is a logical next step to take, and is the subject of our current research (Kitchell et al. 1986).

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Appendix

Harvest and CPUE time paths for each future state–policy combination. Catch figures are in thousands of kilograms; CPUE figures are kilograms per unit of effort. Listed below each policy is the future biotic state (in parentheses). Actual CPUEs are used for the year 1983. Gill net CPUE is catch per 305.6 m (1000 ft) of gill net lifted; drop net CPUE is catch per pot lifted. Each drop net has two pots.

	Rehabilitation (optimistic–fast)			Rehabilitation (optimistic–slow)		
Year	Catch	Gill net CPUE	Drop net CPUE	Catch	Gill net CPUE	Drop net CPUE
1983	91	6.40	5.03	91	6.40	5.03
1984	159	10.09	9.00	159	9.00	8.60
1985	159	11.18	9.40	159	9.00	8.60
1986	178	12.27	9.80	136	10.45	9.13
1987	197	13.36	10.20	136	11.90	9.66
1988	216	14.45	10.60	170	13.35	10.19
1989	235	15.54	11.00	204	14.80	10.72
1990	254	16.63	11.40	238	16.25	11.25
1991–2007	272	17.70	11.80	272	17.70	11.80

	Rehabilitation (moderate–fast)			Rehabilitation (moderate–slow)		
Year	Catch	Gill net CPUE	Drop net CPUE	Catch	Gill net CPUE	Drop net CPUE
1983	91	6.40	5.03	91	6.40	5.03
1984	159	9.54	8.80	159	9.00	8.60
1985	159	10.08	9.00	159	9.00	8.60
1986	173	10.62	9.20	136	9.73	8.87
1987	187	11.16	9.40	136	10.46	9.14
1988	201	11.70	9.60	163	11.19	9.41
1989	215	12.24	9.80	190	11.92	9.68
1990	229	12.78	10.00	217	12.65	9.95
1991–2007	244	13.35	10.20	244	13.35	10.20

	Rehabilitation (pessimistic–sport favored)			Rehabilitation (pessimistic–commercial favored)		
Year	Catch	Gill net CPUE	Drop net CPUE	Catch	Gill net CPUE	Drop net CPUE
1983	91	6.40	5.03	91	6.40	5.03
1984	159	9.00	8.60	159	9.00	8.60
1985	159	9.00	8.60	159	9.00	8.60
1986	136	9.00	8.60	136	9.00	8.60
1987	136	9.00	8.60	136	9.00	8.60
1988–2007	136	9.00	8.60	217	9.00	8.60

	Baseline (all future biotic states)		
Year	Catch	Gill net CPUE	Drop net CPUE
1983	159	6.40	5.03
1984	242	9.00	8.60
1985	242	9.00	8.60
1986–2007	217	9.00	8.60

Bioeconomic Model of the Lake Michigan Alewife (*Alosa pseudoharengus*) Fishery[1]

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Hanson, F. B. 1987. Bioeconomic model of the Lake Michigan alewife (*Alosa pseudoharengus*) fishery. Can. J. Fish. Aquat. Sci. 44 (Suppl. 2): 298–305.

A stochastic bioeconomic model is developed for the Lake Michigan alewife (*Alosa pseudoharengus*) fishery. This theoretical model possesses an intermediate degree of complexity and realism. Other Lake Michigan fish stocks are included in a simplified way as an aggregate, to account for interspecific predation by salmonids, but competition could be treated as well. Both alewife and aggregate fisheries are modeled by modifications of Beverton–Holt single-cohort models with growth in weight and interspecific interactions. The alewives are also subjected to large random disasters and it is demonstrated that these are density independent. The methodology is stochastic, feedback, optimal control using dynamic programming. Stochastic terms are used to represent random disasters in the alewife population. The computational results are given in terms of the maximal, expected economic values of the combined fishery and the optimal rates of harvest for both the alewives and aggregate fisheries. These results are new in the sense that continuous dynamic programming has been applied to a model for several interacting species undergoing occasional random shocks. The expected, optimal economic value of the combined fishery is much less sensitive to the initial recruitment of alewives than to that of the salmonid aggregate. Comparison with a deterministic model that does not include the random disasters shows that the disasters reduce the economic value of the combined fishery by 10–15%. The results are sensitive to reasonable data estimates and confirm the overexploitation of alewives by both the alewife fishery and salmonid predation. The need for reliable data with a common basis is emphasized with regard to comparing commercial and sport fisheries.

L'auteur élabore un modèle bioéconomique stochastique de la pêche du gaspareau (*Alosa pseudoharengus*) du lac Michigan. Ce modèle théorique est d'un niveau de complexité et de réalisme intermédiaire. Les autres stocks de poisson du lac Michigan y sont inclus d'une façon simplifiée, en tant que groupe, afin de tenir compte de la prédation interspécifique par les salmonidés, mais on pourrait aussi tenir compte de la compétition. Les pêches du gaspareau et les pêches regroupées sont modélisées par modification des modèles à une seule cohorte de Beverton–Holt tenant compte de la croissance pondérale et des interactions interspécifiques. Les gaspareaux sont aussi sujets à d'importantes catastrophes aléatoires et l'on démontre que ces dernières sont indépendantes de la densité. La méthodologie utilisée est stochastique et fait appel à la rétroaction et au contrôle optimal par programmation dynamique. Des termes stochastiques servent à la représentation des catastrophes aléatoires affectant la population de gaspareaux. Les résultats sont présentés en termes des valeurs économiques maximales prévues de la pêche mixte et des taux optimaux de récolte des pêches du gaspareau et des pêches regroupées. Les résultats obtenus sont originaux en ce sens que la programmation dynamique continue a été appliquée à un modèle portant sur plusieurs espèces présentant des interactions et subissant à l'occasion des chocs aléatoires. La valeur économique prévue optimale de la pêche mixte est beaucoup moins sensible au recrutement initial des gaspareaux que celle du groupe des salmonidés. La comparaison avec un modèle déterministe ne comprenant pas de catastrophes aléatoires montre que ces dernières réduisent la valeur économique de la pêche mixte de 10 à 15 %. Les résultats réagissent à des estimations de données raisonnables et confirment la surexploitation du gaspareau par la pêche du gaspareau et la prédation par les salmonidés. L'auteur met l'accent sur la nécessité d'obtenir des données fiables à base commune pour la comparaison des pêches commerciale et sportive.

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The alewife (*Alosa pseudoharengus*) is an exotic, warm-water fish that invaded the Great Lakes from the Atlantic Ocean. They were first noticed in Lake Michigan in 1949 (Miller 1957). The role that exotic marine invaders such as the alewife and sea lamprey (*Petromyzon marinus*) have played in altering the Great Lakes ecosystems was discussed in much detail by Smith (1968, 1970, 1972), Brown (1968, 1972), Wells and McLain (1973), Christie (1974), Francis et al. (1979), and Crowder (1980).

There are substantial Atlantic commercial alewife fisheries (Smith 1970). In the Great Lakes, only in Lake Michigan is there a substantial alewife fishery. From 1966 to 1977, the Lake Michigan alewife fishery has contributed from 60 to 90% of the total Lake Michigan commercial catch by weight (Fig. 1), according to the data compiled by Baldwin et al. (1979) and supplemented by Wells and McLain (1973). During the same period, the proportion of the total Great Lakes catch made up of alewives by weight was 20–40%. However, the commercial value of the alewife catch is low, about \$0.02/lb. (\$44/metric ton). The commercial fishery is also dominated in value by chubs (*Coregonus* spp.), whitefish (*C. clupeaformis*) and rainbow smelt (*Osmerus mordax*) along with the alewife, although it takes a lot of alewife to have comparable value to the others. In turn, the sport fishery involves much more total economic benefit than the commercial fisheries. Still, the alewife fishery contributed a very important component to the Great Lakes commercial catch in terms of weight, but this was not so prior to the later part of the 1960s. According to Samples and Bishop (1982) the commercial alewife landings have significantly declined to their 1964–65 levels in 1980 partly as a result of increased stocking of salmonids (such as lake trout (*Salvelinus namaycush*), rainbow trout (*Salmo gairdneri*), brown trout (*S. trutta*), chinook salmon (*Oncorhynchus tshawytscha*) and coho salmon (*O. kisutch*)). Recent catch data compiled by the Great Lakes Fisheries Commission (1451 Green Bay Rd., Ann Arbor, MI 48823, USA) for the years from 1978 to 1983 show that the alewife catch has dropped, but is still around 50–60% of the total Lake Michigan catch by weight (Fig. 1). Brown et al. (1987) show that the previously depressed chub population has become the dominant forage fish in terms of biomass relative to the alewife and the rainbow smelt.

The Lake Michigan alewife is used primarily for fish meal or fertilizer and is not directly used for human consumption. However, the presence of the alewife and the alewife fishery has a profound indirect effect on human consumption of fish. Bishop and Samples (1980) and Samples and Bishop (1982) cited the conflicts between the commercial alewife fishery and the Lake Michigan sport fishery because the alewife is a principal source of forage for the salmon and trout primarly desired by the sport anglers. The sport versus commercial fishery conflict was discussed in more general context by Talhelm (1979), McConnell and Sutinen (1979), Samples and Bishop (1981), and Copes and Knetch (1981).

An important biological feature regarding the alewives is that they suffer from occasional massive mortalities and litter the beaches of the lakes. Brown (1968) discussed the massive die-off of 1967. Many causes are suggested for the massive die-offs such as fungal infection, noxious algal blooms, hemorrhages, or the inability to adapt to severe temperature changes. Brown (1968) suggested the latter as a more plausible explanation for these massive mortalities. Heufelder et al. (1982) studied the thermal shock due to upwelling of cold water in Lake Michigan on the larval alewife distribution. The alewives are

FIG. 1. Fluctuations in the Lake Michigan alewife fishery (lower curve) compared with the total Lake Michigan catch (upper curve) by weight.

clupeoids, a family of fish including herring and anchovies that exhibit wide fluctuations in population levels and even collapses, according to Murphy (1977). The inclusions of collapses in the present bioeconomic model is the main contribution of this paper.

Crowder (1980) concluded that the alewife, together with rainbow smelt, probably caused the decline of many species native to Lake Michigan through predation on larvae and the consumption of eggs. The alewives, when all details are considered, interact on several trophic levels. They are competitors with regard to consumption of food for the young of other fish. They prey on the eggs and young of other species and they are the prey of salmonids. Predation by alewives appears to be more important that competition by alewives with regard to species on the decline.

The scarcity of higher level predators prior to 1965 caused the alewife population to explode due to lack of predatory regulation. The sea lamprey, prior to being brought under control, played the role of the topmost marine predator, preying on potential predators of the alewife. Stewart et al. (1981, 1983), Eck and Brown (1985), and Eck and Wells (1987) emphasized the important role that alewives have played as a forage base for Lake Michigan salmonids during the past decade and as a limitation to the expansion of the salmonid sport fishery in the future. Eck and Brown (1985) reported that 71% of the diet of Lake Michigan lake trout in 1979 was alewives. Stewart et al. (1981) made similar estimates for coho and chinook salmon. Samples and Bishop (1982) have noted that the surge in stocking salmonids in Lake Michigan in recent years has had an impact on the recent decline and the associated drop in commercial landings of alewives. These declines are in part attributed to the increased predation pressure by the growing number of salmonids on the alewives, without strong evidence of switching to other prey as the alewives have declined. It should be noted for completeness that the alewife fishery has also been strongly affected by polychlorinated biphenyls (PCB) and other forms of contamination in several markets (Bishop 1982) and by the fact that it is a highly demand-driven fishery, depending on the worldwife supply of fish meal and other products. These latter

complications are beyond the scope of current modeling techniques.

Bishop and Samples (1980) and Samples and Bishop (1982) have studied the deterministic optimal control of a theoretical harvesting model for the commercial alewife fishery and the salmonid sport fishery, coupled together by predator–prey relations. Their method involves the maximum principle and their main results are restricted to the steady-state case. Related multispecies, multiuser deterministic models have been investigated by Clark and Kirkwood (1979) and Charles (1983) with applications to an Australian prawn fishery. In addition, Clark (1980, 1982) has analyzed the connections to the economic regulation of multiuser fisheries.

In the next section a stochastic bioeconomic optimal control model is described for the alewife–salmonid prey–predator system. The deterministic component of this model has a significant intersection with the predator–prey harvesting model of Bishop and Samples (1980) and Samples and Bishop (1982). The stochastic component represents the random die-offs in the alewife population. However, the current computational approach permits us to calculate results for either the deterministic or stochastic dynamic model as in Ryan and Hanson (1986). In the Results section the stochastic optimal feedback control results for the dynamic system are discussed. A comparison of both stochastic and deterministic results is also presented.

The Dynamic Model

The entire alewife ecosystem and related economics are much too complex to model in a form that can be reasonably analyzed. Even though the alewife catch has declined in absolute terms, it is still a significant fraction of the total Lake Michigan catch in terms of biomass. Hence, a bioeconomic model of intermediate degree of complexity is proposed that retains some of the important features of the much larger, more realistic system. Let $B_1(T)$ denote the biomass of alewives in the lake at time T and $B_2(T)$ denote the biomass of the aggregate of other fish that interact with the alewives. The symbol B, without subscripts, will denote the vector of biomasses (B_1, B_2). The dynamic model is based on Beverton and Holt (1957) single-cohort models for both alewife and aggregate. Growth in weight terms, interaction terms, and random perturbation terms are added to the single cohort terms. The alewife equation is given by

$$(1)\quad dB_1(T) = (G_1 - M_1 - F_1 - A_1(B)\cdot B_2(T))\cdot B_1(T)dT - b_1\cdot B_1(T)dP_1(T, f_1)$$

and the equation for the aggregate interactors is given by

$$(2)\quad dB_2(T) = (G_2 - M_2 - F_2 - A_2(B)\cdot B_1(T))\cdot B_2(T)dT - b_2\cdot B_2(T)dP_2(T, f_2)$$

during the fishing season $0 < T < TF$. A simple deterministic predator–prey model would be obtained by setting $b_1 = 0 = b_2$, so that the last term of both (1) and (2) would not appear. This will be discussed in more detail later. The initial conditions specify the population levels,

$$(3)\quad B_1(t) = X_1 \text{ and } B_2(t) = X_2,$$

of both interactors at a starting time t, $0 \le t \le T$. The time t needs to be otherwise arbitrary in order to apply the method of dynamic programming. As a simplified example, constant recruitment levels, $B_1(0) = R_1$ and $B_2(0) = R_2$, could be assumed for both, including stocked fish in the salmonid aggregate case.

Linear weight growth G_iB_i with $G_i > 0$, linear natural mortality M_iB_i with $M_i > 0$, and linear fishing mortality F_iB_i with $F_i = q_iE_i$ are assumed. Here, q_i is the catchability and E_i is the effort.

Linear mortality in the dynamics (i.e. exponential mortality in the biomass) is a common assumption during a single fishing season for postrecruitment fisheries models and is consistent with the conclusions of Stewart et al. (1981) and Eck and Wells (1987) (see also Ricker (1975), Clark et al. (1973), or Clark (1976), for instance). The growth term along with the biomass description, as opposed to only linear mortality terms with a population numbers description, is important to ensure that some positive economic value can be found. The fact that the fishing season will typically be less than 1 yr makes the use of nonlinear terms for growth and mortality unnecessary. In the long run, nonlinear terms for these factors would be needed. However, then the model would need more drastic changes than using nonlinear terms in order to achieve consistent realism. A nonlinear stock recruitment and the interactions with important competitors and others would be needed. Such a long-term model would be far beyond the capabilities of conventional computing facilities at this time. The author is currently working on developing computational methods to handle bigger, more realistic models using advanced computers, but practical results are not available now.

The species interaction terms, $-A_i(B)B_iB_{i'}$, with $i' \neq i$, are by their nature inherently nonlinear. It is assumed that $A_1(B) > 0$ in order to exclude symbiosis. In the case that $A_2(B) < 0$, then B_2 represents a "predator-dominated aggregate"; when $A_2(B) > 0$, B_2 represents a "competitor-dominated aggregate." For the alewife–salmonid system, a "predator-dominated aggregate" is assumed, but this assumption is not critical for the validity of the computational procedure. According to Stewart et al. (1981), the consumption of alewives by salmonids is fairly independent of alewife biomass. Hence, we use a "nearly hyperbolic" functional response with $A_1(B) = A_1'/(A_1'' + B_1)$ with the constant A_1'' small compared with typical alewife biomass. For lack of better data, it will be assumed that $A_2(B) = A_2'$ is independent of B_1 and B_2, so that the predator response will be purely bilinear.

Thus far the deterministic terms of the dynamic model, (1) and (2), have been explained. The corresponding dynamic model of Samples and Bishop (1982) is a quite general deterministic two-species model. More economic details are discussed in their earlier paper, Bishop and Samples (1980). The deterministic terms (b_1 and $b_2 = 0$) of (1) and (2) are but a special case of their model. Their restrictions on general growth–mortality functions (Samples and Bishop (1982)) reduce here to $A_1' > 0$, assuming $A_1'' > 0$ and $A_2' < 0$, i.e. satisfy standard predator–prey relations, with an increase of predators having a negative effect on the growth of the prey, and with an increase of prey having a positive effect on the growth of the predators. Their goal was a static, theoretical analysis and their bioeconomic results would be applicable to other harvested single-predator, single-prey systems. The goal here is a more practical computational study, and hence more specialized for the alewife and salmonid case. However, the present dynamic model is more general in that it is not static and contains stochastic terms, motivated by the occasional mass mortalities in the alewife population.

The final terms, $-b_iB_iDP_i$, in (1) and (2) represent density-independent random disturbances, with $B_1 > 0$ to simulate the massive die-offs of the alewives. In Fig. 2 the significant die-offs (change >10%) are presented to roughly show that for this small sample of five die-offs in 1971–72, 1975–76, 1979–80,

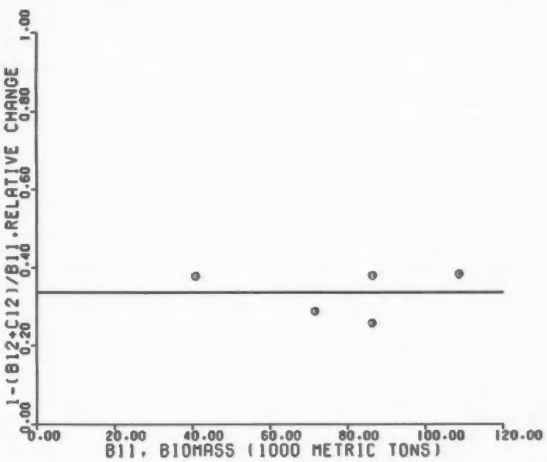

FIG. 2. Evidence of density independence for significant alewife die-offs during 1968–83. B_{11} is the alewife biomass before a die-off, and B_{12} and C_{12} are the biomass and catch, respectively, following a die-off.

1981–82, and 1982–83, die-offs are density independent. In Fig. 2, the relative change, $(B_{12} + C_{12})/B_{11}$, at each die-off is displayed. The B_{11} is the biomass level before a die-off, and $B_{12} + C_{12}$ is the biomass after the die-off corrected by the catch which usually occurs after the die-off. The second subscript is 1 when it denotes the state prior to the die-off and is 2 for the state following the die-off. The biomass data are only available after the big 1967 die-off in Hatch et al. (1981) and Eck and Wells (1987), and only as an annual census. Hence, the data indicate that the die-offs, being density independent, are likely to be from abiotic causes, rather than from biotic causes such as the density-dependent epizootics described by Sindermann (1970). While other random forms might be used, the most appropriate form for the data is to take $dP_i(T, f_i)$ to be an incremental Poisson process with rate f_i, with common values for both infinitesimal mean and variance:

$$\text{(4)}\quad \text{MEAN}[dP_i] = f_i dT = \text{VAR}[dP_i].$$

Hence, $dP_i(T, f_i) = P(T + dT, f_i) - P(T, f_i)$ is just the differential of the well-known, continuous-time Poisson process $P(T, f_i)$ whose distribution is $\exp(-f_iT)\cdot(f_iT)^k/k!$ When $dP_i(T, f_i)$ has the standard Poisson jump of unity with mean frequency f_i, the term $-b_iB_i dP_i(T, f_i)$ causes a jump of amplitude $-b_iB_i$ in the biomass level B_i. The random shocks are exponentially distributed with regard to waiting time between shocks. The conditional mean for the stochastic differential equations, (1) and (2), using (4) are given by

$$\text{(5)}\quad \text{MEAN}[dB_i(T)|B_1, B_2] = (G_i - M_i - F_i - A_i(B)B_{i'}, - b_if_i)B_i dT.$$

The Poisson noise approximation has been applied to the problem of extinction of single-species populations undergoing disasters by Hanson and Tuckwell (1978, 1981). The use of the incremental Poisson process in single-species bioeconomic models was made by Ryan and Hanson (1985, 1986). As an example of other forms of random noise, we mention that Ludwig (1980) investigated the effects of Gaussian noise on single-species harvesting strategies. However, Gaussian "white" noise, being continuous, would be unsuitable to model mass mortalities, in contrast with Poisson "white" noise.

The economic objective is to determine the optimal, expected present value of the combined alewife and aggregate resources. The discounted, present value is given by

$$\text{(6)}\quad V[B, t, E, P] = \Sigma_i \int_t^{TF} dT \exp(-\delta_i\cdot T)E_i(B, T)\cdot[p_iq_iB_i(T) - c_i - \epsilon_i\cdot E_i(B, T)]$$

where p_i is the price per unit of harvested biomass and $(c_i + \epsilon_i\cdot E_i)$ is the cost per unit of effort, with $i = 1$ denoting the alewives and $i = 2$ denoting the predatory aggregate. The symbol Σ_i denotes the sum over both prey and predator. The linear cost is denoted by c_i, and the quantity ϵ_i is a quadratic cost factor that we set to be small here, to approximate the linear cost limit while leaving other computed quantities to be well defined as in Ryan and Hanson (1986). However, quadratic costs are very reasonable because increased effort usually leads to greater inefficiencies due to the use of more inefficient gear and congestion on the fishing ground, cited as crowding externalities by McConnell and Sutinen (1979). Note that the cost per unit harvested biomass is $(c_i + \epsilon_i\cdot E_i)/(q_iE_iB_i)$ and thus is population dependent. Technological independence, in the sense of Anderson (1975), is assumed because dB_i is independent of E_j when $i \neq j$. The effort is selected as the feedback control variable rather than the fishing mortality, F_i, because the effort, E_i, can be directly related to the actual gear used and can be related to F_i through the catchability coefficient, q_i. The factor δ_i is the effective discount rate that expresses the time preference for alternative investments. The population level of species i, $X_i = B_i(t)$ given in (3), is specified at the arbitrary starting backward time t in order to derive the equation of dynamic programming. Using the more general starting population level X_i, the dynamic programming results are applicable to more general situations, including those in which X_i is recruitment or newly stocked fish. In (6), the quantitites B, X, E, and P are used without subscripts to indicate vector entities whose components have subscripts.

The optimal, expected present value is denoted by

$$\text{(7)}\quad V^*(X, t) = \text{MAX}_E[\text{MEAN}_P[V[B, t, E, P]|B(t) = X]],$$

subject to the dynamic constraints given in (1) and (2), as well as the control or effort constraints

$$\text{(8)}\quad 0 \leq E_i(X, t) \leq E_{\max,i} \quad \text{for} \quad i = 1 \text{ or } 2.$$

Application of a generalized chain rule applied to (1) through (7) leads to the Bellman equation appropriate to dynamic systems perturbed by Poisson processes (see, for instance, the single-species applications in Hanson and Ryan (1984, 1985) and Ryan and Hanson (1985, 1986):

$$\text{(9)}\quad V^*_{,t} + \Sigma_{i\neq i'}[G_i - M_i - A_i(X)X_{i'}]X_iV^*_{,X_i} + f_1\cdot[V^*((1 - b_1)X_1, t) - V^*] + f_2\cdot[V^*((1 - b_2)X_2, t) - V^*] + S(X, t), \quad X_1 > 0, X_2 > 0, 0 < t < TF$$

where $V^*_{,t}$ and $V^*_{,X_i}$ denote the first partial derivatives of V^* with respect to t and X_i, respectively. Note that the Poisson disaster term in the dynamics gives rise to a delay term, with the $(1 - b_i)X_i$ argument, in the Bellman equation. However, the optimization of the integral objective, defined in (6) and (7), is

reduced to a simpler objective given by the switch term:

$$(10)\quad S(X, t) = \mathrm{MAX}_E[\Sigma_i \exp(-\delta_i t)E_i[(p_i - V^*_{X_i} \exp(\delta_i t))\cdot q_i X_i - c_i - \epsilon_i E_i]].$$

The features of the dynamic or biological aspects of the current model without stochastic effects have been compared above with that of Samples and Bishop (1982). In order to compare the features of the full bioeconomic model, principally (1), (2), (6), and (7), with that of Samples and Bishop, the stochastic terms are temporarily assumed to be absent, by removing the means and setting $b_1 = 0 = b_2$. In (9), only the terms multiplied by f_1 and f_2 would be gone. Note that Samples and Bishop used the Hamiltonian or maximum principle formulation that is useful only for the deterministic case, in contrast with the dynamic programming formulation used here. Dynamic programming is directly valid for both the deterministic case and the stochastic case. With the focus on the deterministic version, the Samples and Bishop theoretical conditions on the marginal net economic benefits derived for the total benefits in (6) reduce here to positive linear and quadratic cost coefficients, i.e. $c_1 > 0$, $c_2 > 0$, $\epsilon_1 > 0$ and $\epsilon_2 > 0$, assuming nonnegative effort constraints as in (8). Their benefit conditions, in words, require that the marginal net benefits for both prey ($i = 1$) and predator ($i = 2$) are increasing functions of biomass, B_1 and B_2, and decreasing functions of harvest rate, $h = q_1E_1B_1$ and $g = q_2E_2B_2$.

Hence, the deterministic version of the present bioeconomic model is the specialization of Samples and Bishop's (1982) model. In their papers (see also Bishop and Samples (1980), they examined only theoretical steady-state or equilibrium properties of the solution of their more general deterministic bioeconomic predator–prey model for general rules. However, the steady state is not very practical for the highly variable state of the Lake Michigan environment, nor is it valid for the present stochastic case which models the occasional mass mortality suffered by the alewife. The present model is more specifically tuned to the alewife–salmonid case, yet is more general in that it includes stochastic and dynamic effects.

In the results given below, a comparison of the present stochastic bioeconomic alewife–salmonid model with its deterministic counterpart is obtained by setting $b_1 = 0 = b_2$. In this way, the negative effects of occasional alewife die-offs can be gauged. In a previous paper, Ryan and Hanson (1986) compared stochastic results for a single-cohort model with another deterministic approximation, called the "quasi-deterministic" approximation. This latter approximation included the average disaster term, $-f_1b_1B_1dT$, from (5), so that, for instance, the alewife dynamics becomes $dB_1/dT = (G_1 - M_1 - A_1B_2 - f_1b_1)B_1$. The quasi-deterministic approximation can be used to give a close approximation to the average stochastic results and is appropriate for continuous-type noise such as Gaussian noise. The deterministic approximation that is used here is a better gauge of the full effect of the occasional die-off, in terms of both frequency, f_i, and magnitude, b_i.

Results

In this section, the computational results are presented for the optimal, expected present value, $V^*(X_1, X_2, t)$, and the associated optimal feedback controls, $E_1^*(X_1, X_2, t)$ *and* $E_2^*(X_1, X_2, t)$, of the alewife aggregate–prey–predator system. Knowledge of the optimal controls, $E_i^*(X_1, X_2)$, is perhaps more important than knowledge of the optimal value. Given the current population levels (X_1, X_2) at each time t, the fisheries managers can determine the amount to be harvested at rate E_i^* for species or aggregate i in order to maximize the total expected value or benefit during the fishing season. This in turn alters the population level, and hence "feeds back" on the system.

The time horizon and fishing season is assumed to be $TF = 0.75$ yr. The deterministic, biological, and economic parameters have been deduced from the data of Brown (1972), Stewart et al. (1981), and Samples and Bishop (1981, 1982). Reasonable guesses were required for some items, until better data become available. The parameter values used in (9) and (10), with Kt denoting 1000 metric tons, M$ denoting 1 million U.S. dollars, and M trips denoting 1 million trips, are tabulated below:

Parameter	Alewife value ($i = 1$)	Salmonid value ($i = 2$)
G_i	0.80/yr	1.20/yr
M_i	0.10/yr	0.50/yr
A_i	(0.03/yr)/(10 Kt + B_1)	−0.03/(Kt yr)
q_i	0.0003/trip	0.18/(M trips)
p_i	M$0.044/Kt	M$2.90/Kt
c_i	$200/trip	M$1.18/(M trips)
$E_{\max,i}$	200 trips/yr	0.86M trips/yr
R_i	75 Kt	34 Kt
b_i	0.34	0.00
f_i	0.29/yr	0.00/yr
δ_i	0.07/yr	0.02/yr
ϵ_i	$0.10/((trip)^2/yr)	M$0.50/((M trips)^2/yr)

The discount rate, δ_1, for the alewife is taken to be 7%, while 2% is used for the salmonid sport fishery. In the latter, the rate could just as well be zero because there is little opportunity in the sport fishery to switch to another "investment," except for the investment of the states in their stocking programs.

The economic data of the two fisheries are not very comparable, due to lack of a common basis for economic measurements between the commercial and sport fisheries. In the commercial alewife fishery, the price is the ex-vessel price at the docks, and costs include labor and gear operating expenses. It is important to keep in mind the low value of the alewife compared with that of the sport fish. The commercial costs had to be estimated because they were not readily available. In the sport fishery, the costs are derived in Samples and Bishop (1981) using public costs, principally from stocking salmon and trout, averaged over the number of angler fishing trips; the price is determined by the "travel costs approach" from expenditures that the sport fishers make in the process of catching fish.

The stochastic parameters, b_1 and f_1, were selected from the mean line in Fig. 2 and from the mean frequency of significant die-offs. The salmonid aggregate suffers little from fluctuations compared with that of the alewife population; hence, we set $b_2 = 0 = f_2$.

Figure 3 shows the variation of the optimal, expected value, V^*, with respect to the alewife starting size, X_1, at time t, relative to the total recruitment, R_1. The uppermost curve has the parameter $t = 0$ which decreases by $0.2\cdot TF$ in succeeding curves until the final condition $V^* = 0$ is attained at $t = TF$. The starting salmonid biomass is assumed to start at $X_2 = R_2/2$ for this figure. V^* is somewhat independent of X_1/R_1, especially for the curves closer to $t = TF$ (Fig. 3), reflecting the low value of

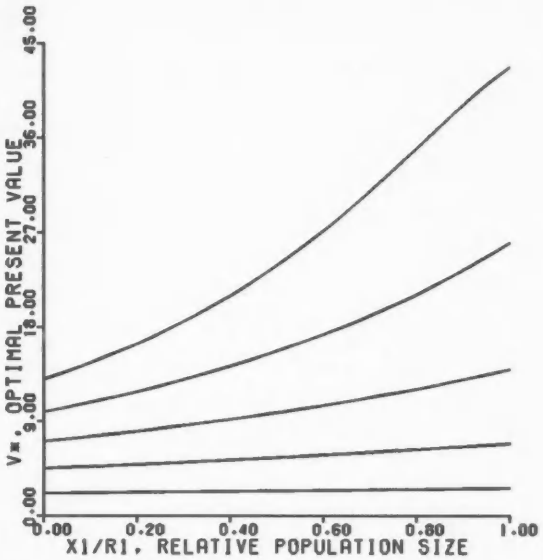

FIG. 3. Optimal, expected present value of the combined fisheries as a function of alewife biomass relative to recruitment biomass. Here, $X_2 = R_2/2$ is fixed and $t/TF = 0$, 0.2, 0.4, 0.6, 0.8, and 1 with the $t = 0$ curve being the uppermost curve.

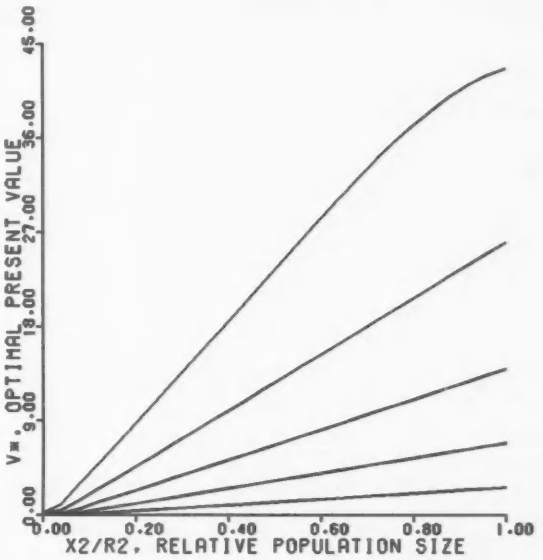

FIG. 4. Optimal, expected present value of the combined fisheries as a function of the aggregate or salmonid biomass relative to recruitment (stocked) biomass. Here, $X_1 = R_1/2$ is fixed and $t/TF = 0$, 0.2, 0.4, 0.6, 0.8, and 1 with the $t = 0$ curve being the uppermost curve.

an alewife harvest compared with the sport fishery. Note that there is still a positive value when $X_1/R_1 = 0$ because there is still much value in the sport fishery in absence of the alewife. Each curve for a given t, besides representing an intermediate value V^*, also represents a V^* for the shorter time horizon, $TF - t$, or fishing season on the same graph. The optimal effort, E_1^*, in harvesting the alewife is not shown due to lack of space, but the positive effort is concentrated within 30% of the final time, $t = TF$. This is because the only positive gain in the alewife dynamics (3) is due to growth in weight, and it is advantageous to wait until the end of the season to obtain the most benefit.

Figure 4 shows the variation of the optimal, expected value V^* with respect to the relative salmonid aggregate starting size of X_2/R_2. As in Fig. 3, the uppermost curve corresponds to $t = 0$, and each successively lower curve corresponds to a time decrement of $0.2 \cdot TF$, with $V^* = 0$ corresponding to $t = TF$. In this figure the alewife biomass is fixed at $X_1 = R_1/2$. Relative to Fig. 3, in general, V^* exhibits much more sensitivity to X_2/R_2 than to X_1/R_1, with a nearly linear relationship for the values of t closer to TF. There is almost no economic value in the system of small values of X_2/R_2, reflecting the higher economic value of the salmonids compared with the alewife. The contrast in behavior is the result of the fact that the commercial fishery has low profitability at a price of \$0.02/lb. (\$44/metric ton), while the sport fishermen place a high value on the recreational aspects of the sport. This economic comparison of the two fisheries is very fluid because the sport fishery economics rest on subjective evaluations. The salmonid optimal effort, while not shown, is at the maximal level, $E_{2,\max}$, for all but the lower salmonid biomass levels, i.e. $X_2/R_2 > 0.2$. In contrast with the alewife, the salmonid is positively affected by both weight gain and the consumption of alewives.

Figure 5 shows the effect of random massive mortalities in lowering the optimal, expected, total present value of the combined fisheries versus the relative alewife biomass, X_1/R_1, with $t = 0$ and $X_2 = R_2/2$. The upper curve is the deterministic case without any occasional, random massive alewife mortalities ($b_1 = 0$), while the lower curve is the stochastic case as in Fig. 3. The random die-offs cause a decrease from the deterministic value of about 15% at $X_1/R_1 = 0$ to under 11% at $X_1/R_1 = 1$.

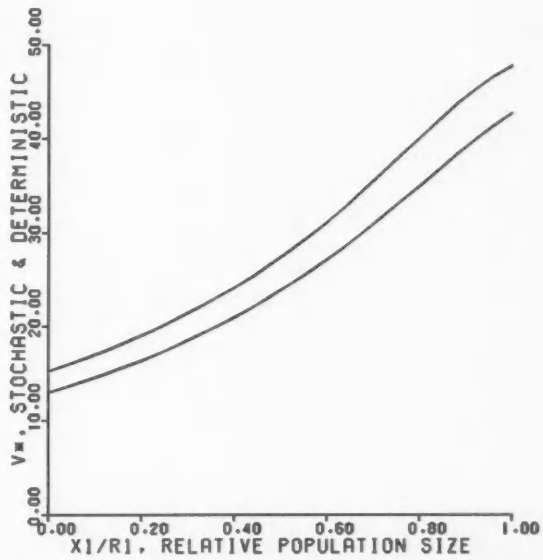

FIG. 5. Comparison of stochastic and deterministic, optimal present values at $t = 0$ and $X_2 = R_2/2$. The upper curve is the deterministic result, which does not include the effects of occasional, random die-offs, and the lower curve is the stochastic result.

However, the optimal efforts in the two cases, not shown, are very similar, with most of the positive effort concentrated within 30% of the final time TF.

Discussion and Conclusions

The principal feature of the present results is that they are for the stochastic dynamic system in (1) and (2) with economics in (6), rather than for the steady state of a deterministic dynamic system. They corroborate the steady-state conclusions of Samples and Bishop (1982) that there appear to be more benefits in increasing the salmonid sport fishery at the sacrifice of the commericial alewife fishery, due to the slow increase in the contribution that the alewife fishery makes to the total value of the combined fishery system. The occasional, random massive mortalities of the alewives, in effect, can decrease the optimal, expected, total value of the combined fishery by 10–15%. However, with regard to implications for management, experience confirms the need for an integrated economic approach with a common basis, as emphasized by McConnell and Sutinen (1979) and Copes and Knetch (1981).

In addition, the results would be greatly improved with more consistent and reliable data. This is especially important for the predator–prey interaction term A_i, weight growth G_i, recruitment R_i, catchability q_i, linear costs c_i, quadratic costs ϵ_i, and the disaster rate f_i. Some values which appear to be reasonable estimates can lead to unstable results. The alewife data give strong indication that the alewife die-offs are density independent, and thus very likely to be of abiotic origins. More data are needed concerning population levels in the Great Lakes (i.e. data should be collected more frequently than annually) in order to make reasonable estimates of disaster rates. Even more data are required to determine the effectiveness with which the Poisson process models the die-offs. For want of better data, the Poisson assumption appears to be best, and any better replacement is likely to be an empirical distribution. Evidence from the catch data and numerical experiments connected with this study indicates that the alewives are overexploited or overstressed by both the alewife fishery and by the stocked salmonids. For example, the biomass and catch data imply that the catch per unit biomass was a high 45% in 1983.

Possible directions for improving the model would be to include other important interspecific competitors, especially the chubs and the smelt. Economic factors such as variable demand or pollution effects would also be important for the Great Lakes in general. Such improvements would require advances in theoretical, experimental, and computational approaches to the problem.

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Mechanisms Affecting Public Acceptance of Resource Management Policies and Strategies[1]

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Managing the issues which arise from Great Lakes rehabilitation efforts will involve some expertise in psychology and sociology and in the administration of public involvement processes. The components of issues which must be managed include inadequacies in our science, incomplete and/or conflicting public beliefs, and conflicting public values. Decisions must often be made without the benefit of complete scientific information, and the public is poorly prepared to deal with this limitation. Even when scientific knowledge is adequate, segments of the public may be uninformed and create issues. Most issues result from conflicts between users with differing value priorities in a management decision. Public involvement strategies exist to increase representative and interactive participation by citizens needed to resolve or avoid many issues, but additional strategies must be developed to deal with the difficult dynamics of value conflicts. The response of management agencies should be to implement long-range programs to develop their own expertise in the dynamics of public perceptions, citizen skills to participate in the management process, and more effective strategies for involving citizens in the difficult, value-laden resource management process.

Pour régler les problèmes découlant des efforts de remise en état des Grands Lacs, il faudra certaines connaissances spéciales en psychologie et en sociologie ainsi qu'en administration des processus de participation du public. Les insuffisances de la science, les opinions incomplètes ou conflictuelles du public et ses valeurs opposées comptent parmi ces problèmes. Souvent, des décisions doivent être prises sans données scientifiques complètes et le public est mal préparé à accepter cette restriction. Même quand les connaissances scientifiques sont adéquates, certains secteurs du public peuvent être mal informés et causer des problèmes. La plupart de ceux-ci découlent de conflits entre les utilisateurs dont les priorités diffèrent quand il s'agit de prendre des décisions relatives à la gestion. Il existe des stratégies pour accroître la participation représentative et interactive de citoyens, qui permettent de régler ou d'éviter de nombreux problèmes, mais on doit élaborer d'autres stratégies pour venir à bout des difficultés que présentent les valeurs en conflit. Les organismes de gestion devraient, à cette fin, mettre en oeuvre des programmes à long terme pour développer leurs propres connaissances en dynamique des perceptions du public, les aptitudes des citoyens, de façon qu'ils participent au processus de gestion, et élaborer des stratégies plus efficaces pour faire participer les citoyens à la gestion des ressources, processus difficile mais qui a beaucoup de valeur.

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> The purpose of the International Symposium on Stock Assessment and Yield Prediction [ASPY] is to advance the understanding of how aquatic production is best apportioned to maintenance/rehabilitation/surplus production, to achieve optimal fishery productivity and benefits for the Great Lakes community (Christie et al. 1984, p.1).

The above goal cannot be achieved on the basis of biological research alone. The goal itself — "optimal fishery productivity and benefits" — must be defined sociologically as well as ecologically. Even the biological data base used to make necessary yield predictions is influenced by angler behavior (Jenkins and Morias 1971; C. A. Lewis and M. A. Henderson, unpubl. data; Schlesinger and Regier 1982; Schlesinger and McCombie 1983).

The success of many fisheries management programs is dependent on the cooperation of fishers. Healey (1985) has shown the important influence of values held by commercial fishers on the success of a management plan to achieve a stable yield of Atlantic herring. He proposed that while "... little attention has been given to analyzing the behavior of fishermen and how they decide among alternative courses of action ... [their] behavior ... is usually critical to the success or failure of any management regime" (Healey 1985, p. 179).

There are broad important public dimensions to the overall goal of the Great Lakes Fisheries Commission (GLFC) to rehabilitate the Great Lakes. This goal places a high priority on the ecological value of resources. That is, a stable, healthy ecosystem is important as an end in itself. It is probably safe to infer that at the policy level, Great Lakes residents would endorse the rehabilitation of the biosystem of the Great Lakes,

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including self-sustaining lake trout. However, the choices will not be so clearly defined at the implementation level where changes affect regulations, recreational opportunities, economics, and other aspects of human lives.

When rehabilitation strategies are implemented, the impacts on other values become more acute and the "American public" segments into a complex array of public groups, each with its own set of concerns and preferences. Since the actual management unit which must implement rehabilitation plans is at the state or province level, the management goals and processes are vulnerable to the social forces arising from conflicting groups. The political environment of state resource agencies holds increasing public expectations and demands for participation.

This paper will discuss the components of resource issues, the dynamics of public perception and response, and the role of public involvement in implementing management programs. The GLFC objective to achieve self-sustaining lake trout populations illustrates the importance of considering these public dimensions in plans to rehabilitate the Great Lakes.

Nature of Management Issues

The public dimension of fisheries (and wildlife) management has gained the attention of managers recently due to increasing conflicts and disruption associated with increasing public demands for limited resources. Since it is unlikely that efforts to rehabilitate the Great Lakes will be immune to this disruption, the discussion here will focus on the manageable components of issues.

Natural resource issues exist when conflicts arise between groups. It is proposed here that one or more of three important components contribute to such conflicts: the state of the science or technology, what the public believes to be true (public beliefs), and the public values and priorities assigned to those values (Peyton 1985). The extent to which resource issues are satisfactorily avoided or resolved is determined by how well each of these components is managed.

Science/Technology Component

Science serves as an important philosophical basis for decision making in this society, yet the information from science is always tentative and rarely complete. That is not an incrimination of science, but it creates dilemmas for managers in the business of pragmatically applying ecological science to the management of Great Lakes resources.

As we reduce Great Lakes ecology to conceptually manageable scientific models, our capability to predict outcomes of management strategies is limited by the data base and by the variables omitted from the management model. This in itself creates a dilemma for the manager. However, equally important is the perception which resource users have of science, science process, and science credibility.

It is asking much of a user group to accept management plans which present *known* risk to that group's values. The task is more difficult when our science has admittedly not identified all the risks and when even the confidence limits of known risks are questionable. In many cases, the response to these situations by user groups is to doubt the credibility of managers and the scientific basis for management. In such instances the user groups often become disruptive and unaccepting and prefer to impose their own experiences, observations, and intuition as a basis for management. For example, Canadian tuna fishers argued that the biological effects of fishing on tuna stocks were unknown and therefore fishers should be allowed to exploit the stocks fully. They proposed that fishing pressure would be self-regulated because of failing profits when the stocks became scarce (Kafka 1984).

A situation in which commercial fishers did value a scientific basis for management has been described by Pringle (1985). Harvesters of Irish moss on Canada's east coast voted to sacrifice economic gains and turn over one of their harvest sites for research purposes during a critical time of low harvest. Pringle suggests that such positive responses are enhanced when fishers are included in the planning process and understand the scientific basis for decisions. However, in the same article, he reported an instance where harvesters chose to withstand the known economic losses of traditional harvest methods because they mistrusted research data that a new, efficient harvest method would pose no risk to the resource. These examples illustrate the range of attitudes towards science and introduce the role of public participation in achieving public acceptance of scientific management.

The message is clear. A major component of resource issues is the adequacy and nature of our science (Cushing 1974; Walker 1973). An equally important component is the public's perception of science. Often the public does not understand the scientific process, nor the proper use and limitations of science. A common response by resource managers is to "educate" users about the *informational* products of science. Too often the informational products are oversimplifications which create credibility problems later when the oversimplified rule does not apply. Consider, for example, the management implications of convincing anglers that lake trout released after they have been hooked and brought to the surface suffer an excessively high mortality rate. This "scientific fact" has been widely accepted among managers and fishers. The implications are that regulations which require catch and release to allow escapement of reproductive sizes of lake trout will be ineffective. Sport fishers will be reluctant to give up that part of their harvest if they perceive the fish will be wasted. Yet, results of recent studies have indicated that the mortality rate may be less than 15% of fish released (Loftus 1986). If this proves to be the case, catch and release of lake trout is a viable option, but an extensive reeducation of sport fishers (and managers) will be necessary.

We have traditionally ignored the *process* side of science in our education attempts. The public is not exposed to the complexities of the scientific process, nor to the limitations imposed by difficulties of data collection or incomplete experimental design. User groups often face inconvenience and/or economic hardships resulting from fisheries regulations. If they are to maintain a sense of credibility in management programs, they must be helped to develop realistic expectations of the scientific basis of management.

Public Values Component

The values component refers here to "held values" (Brown 1984) and the priorities assigned to those values rather than the more quantitative economic values often applied to natural resources.

Kellert (1976, 1980) has proposed a model of attitudes held toward animals which suggests basic values that can be applied towards any resource. The model indicates that individuals and groups have an array or profile of values toward natural entities. Kellert (1978) found antihunters and hunters to differ in their

attitude profiles due to stronger moralistic and humanistic attitudes among antihunters and stronger naturalistic, utilitarian, and dominionistic attitudes among hunters. The conflict between these groups has little to do with inadequacies in our management science. It is a conflict in these basic values toward animals.

One would expect consumptive users of the Great Lakes to have strong utilitarian values for fisheries resources, but many also have other values for the resource (Pringle 1985). However, important differences in value profiles would be expected between groups of Great Lakes users, for example, sport and commercial fishers. Evidence exists that values held for fish stocks by commercial fishers go beyond purely utilitarian value, but that this is not true for the large processing industries (Pringle 1985). Nonconsumptive users of Great Lakes resources (e.g. boaters and swimmers) may represent still different profiles. Citizens who do not use the Great Lakes directly but either intend to in the future or who just value the existence of the Great Lakes (option and existence values; Talhelm 1984[2]) may have much lower utilitarian and dominionistic values and even higher ecological and/or moralistic values than consumptive groups.

A final group of considerable importance is the Great Lakes managers themselves. Evidence exists that wildlife biologists have value profiles which are different from those of the general public and the clients served by the biologists (Peyton and Langenau 1985). It is likely that differences in values also exist between Great Lakes resource managers and users.

The held values which exist among the public are far more complex than those presented here. However, these comparisons suggest considerable opportunity for conflict resulting from lake trout rehabilitation programs. The strong ecological value reflected by this management goal would be accepted by public groups with strong preservation or protectionist goals. These groups would support the rehabilitation goal because they value the stability of the resulting ecosystem (ecological) and/or because they perceive the lake trout (and ecosystems generally) to have a moral right to exist naturally (moralistic). These allies, however, may eventually become opponents of specific management tactics (e.g. use of TFM, sport fisher harvest of trout). Some sport and commercial fishers may prioritize utilitarian values of the Great Lakes to support a large harvest of hatchery lake trout over the value of a naturally maintained population of lake trout with less harvest opportunity. Their ecological value would also make allies of some segments of this consumptive group in the overall goal of Great Lakes rehabilitation, but their utilitarian values suggest a potential opposition to some of the management strategies.

A major component of most issues associated with lake trout rehabilitation will be conflicting values held by various groups. The fisheries managers have difficult roles in resolving these types of value-related issues. For example, many of these conflicts are questions of resource allocation where the managing agency has the difficult task of prioritizing the values held by competing groups and allocating limited resources accordingly. Often in these cases, biological reasons for allocating resources do not exist. The agency cannot avoid antagonizing some of the user groups unless methods can be found to help them make compromises among themselves.

Managing conflicting value issues will require fishery managers to understand the value priorities of affected public segments. Managers should seek solutions which minimize or mitigate the impacts of management strategies on those affected priorities. Another task is to determine the extent to which groups (and individuals) involved in fisheries issues are aware of their own priorities and consequences (i.e. how well have they thought about all affected values and the consequences). Too often, individuals take advocacy positions without having performed this important process. Management strategies implemented to represent these positions can fail when the unanticipated consequences are opposed by the very groups that had earlier advocated the strategy.

Public Belief Components

In addition to beliefs about science, the beliefs held by the public concerning any aspect of Great Lakes rehabilitation may contribute to management issues. For example, inland stream trout anglers who believe that TFM or barrier dam construction seriously affects trout populations are beginning to create an issue over those methods of lamprey control.

Beliefs and values do not exist independently in the minds of individuals. They influence each other directly and indirectly during the attitude formation process in ways to be discussed later. However, some Great Lakes rehabilitation issues are created by conflicting beliefs even when value priorities are clearly agreed on. For example, sport shop owners and charter boat captains may agree on the importance of decreasing harvest of lake trout to assure necessary escapement (value), but disagree on the types of restriction needed to achieve the biological goal and to provide highest economic benefits (belief).

Conflicts in beliefs are made more complex by the inability of science to provide clear-cut answers. In addition, belief conflicts are usually associated with conflicts in value priorities, so opponents not only disagree on what constitutes facts, but also on what valued aspects of the resource are to be protected or enhanced.

Unfortunately, most issues arising from attempts to rehabilitate lake trout will involve all three components: the state of our science, public beliefs, and public values. Incorporating ways to manage the public belief and value component is no less challenging than the development of an adequate ecological basis for Great Lakes rehabilitation.

Determining Factors of Public Response

Fisheries managers must deal with both attitudes and behaviors of the public in an issue (Fig. 1). Attitudes may be considered as the individual's (or group's) position on the issue (e.g. favor or oppose natural lake trout populations). Behaviors may be expressed as active opposition or support, as compliance or noncompliance, etc. The model in Fig. 1 suggests that an individual's final response to an issue is a function of many factors. It is not a simple linear system in which new information forms an attitude which, in turn, determines the desired response. Behaviors are often not consistent with the attitudinal component. For example, an angler may agree with the need to restrict lake trout harvest, but fail to comply with the

[2]D. R. Talhelm [ed.] 1984. Unrevealed economic values of ecosystem management. Great Lakes Fish. Comm. Unpubl. Tech. Rep. Great Lakes Fishery Commission, 1451 Green Road, Ann Arbor, MI.

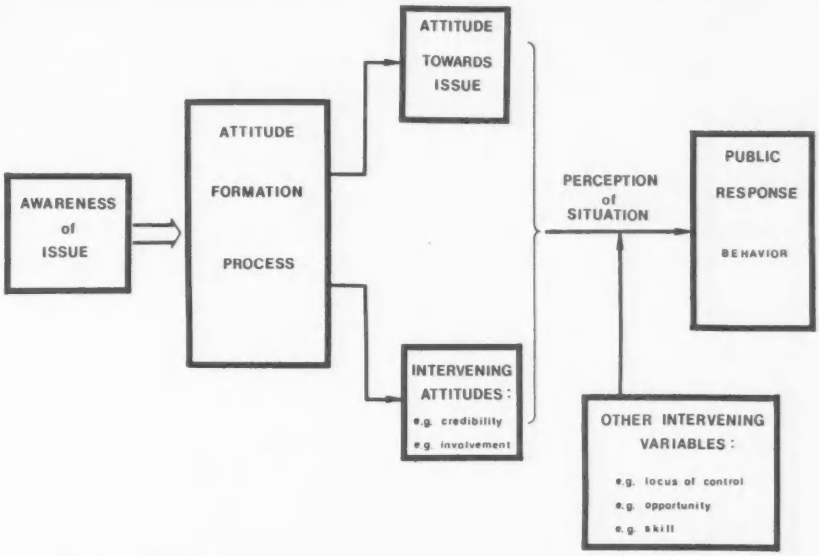

FIG. 1. Role of intervening attitudes and other variables in determining the response of publics to an issue.

regulation. In other situations, citizens who agree with a proposed management program may fail to take appropriate citizen actions to support the proposal. This often allows actively opposed citizens to bias public response and to have a disproportionate influence on decision makers.

In addition to the attitude held towards the specific issue question, other attitudes and factors may influence the final response. The credibility placed on the management agency by a user group may greatly influence acceptance of a regulation by that group (Peyton and Gigliotti 1985). An angler who does not know how to become involved (e.g. through hearings, letter writing, communication channels, etc.) or who does not perceive that such efforts make any difference (locus of control; Fig. 1) may not express support or opposition through citizen action. (A nontechnical discussion of some of these processes and their implications for working with the public is provided by Shafer and Tate (1981).)

Although other factors intervene to determine the final response to lake trout rehabilitation strategies, attitudes remain an important factor. Figure 2 presents many of the processes and components involved in attitude formation.

Attitude formation is an evaluation of some object or situation based on the individual's values and beliefs. Attitudes and values differ in that values are a more fundamental component within a person's makeup than attitudes (Rokeach 1971). Values are enduring standards or preferences which influence choice and action (Brown 1984). Attitudes may change as new priorities are assigned to values or as beliefs are modified by new information, etc.

The model in Fig. 2 indicates that many values are held by an individual. To form an attitude about an issue such as lake trout rehabilitation, an individual must identify relevant values and prioritize them. The consequences to these priorities are then evaluated with existing beliefs. This process may be quite rapid and incomplete, producing an attitude based on unclear priorities and inadequate beliefs, or the process may occur over a longer period and be thorough and rationally developed.

From a resource manager's position it is more desirable to have user attitudes formed by thorough, rational processes even if the products differ from those of the manager. When individuals or groups hastily form attitudes with strong value concerns, they tend to engage primarily in defending those value concerns rather than seeking effective resolution to the issue. Rational consideration of a resource issue may also be inhibited when the issue is presented as such a complex and massive situation that individuals become overaroused and are not capable of innovative, constructive actions (Weick 1984). Weick suggested that issues be reformulated as smaller, manageable problems which can be resolved and which provide a pattern of positive, reinforcing successes for the public. It may be difficult to get definitions of the problem large enough to arouse interest yet not overwhelm the public.

Weick (1984) offered generalizations with implications for the fisheries manager. For example, people highly aroused over a fisheries issue would find it difficult to be creative and resist old patterns of responses. They would be more receptive to information that supports positions they have already taken. Such characteristics run counter to the goal of rational public participation in resource management. Weick suggested that high arousal can be effective in improving participation by citizens who have already been prepared with skills and knowledge.

Complex resource issues may create overarousal, but when people must spend much effort analyzing a complex situation, the issue can become depersonalized and arousal is lowered. Feelings of powerlessness also lower arousal (Weick 1984). Obviously, it is important for managers to plan carefully how they package fishery issues for public participation.

Applying knowledge of public attitudes and behavior to segments of the public will help managers avoid disruptive issues and to increase acceptance of rehabilitation goals and strategies. Marketing segmentation methods can facilitate this process. Market segmentation techniques are recognized by the advertising industry as an effective aid for predicting and

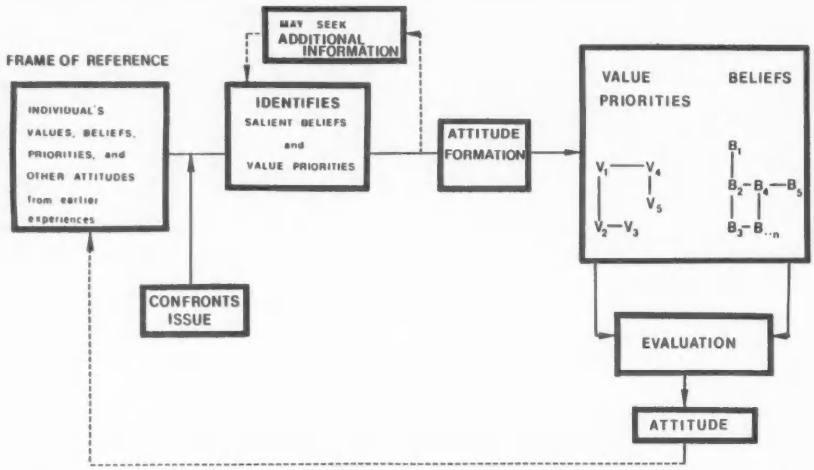

FIG. 2. Attitude formation process results in a complex matrix of beliefs and value priorities. If new information and/or value awareness is accepted, the attitude may be modified.

influencing responses of consumers (Atlas 1984). Driver and Cooksey (1977) have used marketing analysis with sport fishers and argued that the methods hold considerable potential for use in natural resource management. As fisheries managers become more familiar with these approaches, they can be more effective in improving public involvement in and acceptance of management programs.

Even the few principles of attitude formation and behavior discussed here hold several implications for the lake trout rehabilitation effort. General public support for the lake trout proposal will be largely based on ecological values and poorly developed belief systems. Lake trout rehabilitation strategies will not have been evaluated by the general public in terms of impact on economic, utilitarian, and recreational values. Groups (e.g. sport shop owners, charter boat owners, recreational and commercial fishers, etc.) will base their evaluation of rehabilitation on differing values and beliefs. The ecological value basis for lake trout rehabilitation will conflict with the priorities of many groups as rehabilitation strategies are proposed and implemented. The tendency will be for these groups to become polarized and disruptive.

Managing the Public Dimension

Public Acceptance versus Public Involvement

The GLFC has identified the need to gain public acceptance of its rehabilitation goals for the Great Lakes (Francis et al. 1979). However, states are being pressured to first seek public involvement in the development of management goals in order to obtain public acceptance of the programs.

This distinction between public acceptance as a goal and public involvement as a process is important. Public involvement may have a number of goals, including public acceptance. Public acceptance of a management program may be gained by several strategies, including public involvement. Public involvement strategies vary in terms of the amount of influence exerted on the managing agency by the public. Arnstein (1969) has suggested a ladder of participation levels ranging from a level where agencies influence and manipulate citizens, through token control of decision making by the public, to complete citizen control. The consultation method used by Canadian managers has been criticized as a token level which provides little opportunity for the public to influence the planning process (Gerin 1984; Hanson and Lamson 1984; Kafka 1984; Kearney 1984). This criticism could also be made of advisory boards, public hearings, and other token involvement procedures used by resource managers in the United States.

Improved public involvement in Great Lakes management can not only increase public acceptance and decrease disruption, but can improve the management plans, represent a broader range of values, and develop citizenship and responsibility for the Great Lakes resource among the public. Increased public involvement will, of course, increase the necessary investment of time and money. However, these costs may be no greater than the costs of disruptions of management programs by an unaccepting public.

A recent experience of the Fisheries Division of Michigan's Department of Natural Resources (MDNR) illustrates the costs of failing to recognize public interests (A. Wright, Great Lakes Fisheries Program Manager, MDNR, pers. comm.). The MDNR determined that 45 450–90 800 kg of whitefish could be harvested in Lake Huron by commercial fishers without damage to the whitefish stocks. The Fisheries Division developed plans to reintroduce a commercial harvest in Lake Huron. The agency involved state leaders of sportsmen groups who were supportive of the plan, but who did not represent the views of local chapters in the Lake Huron region where the members were directly affected. Local sport fishers overwhelmingly opposed reintroducing commercial harvest and rallied extensive public and legislative support for their cause.

Commercial harvest was eventually reinstated by the MDNR at considerable cost. Public actions delayed the program. Much time and money was invested to work with an aroused, defensive public. Perhaps the greatest cost occurred in the form of lost credibility with the sport fishing public. These losses of trust and confidence will hamper future communications.

Principles for Public Involvement and Acceptance

Some of the principles to be considered when involving the

public are discussed here. Sewell and Coppock (1977) and Lamson and Hanson (1984) developed these and other considerations further.

Since humans tend to resist change and avoid risk, a common response by the public to a proposed management plan is to opt for the status quo and to reject the new. When an agency presents its own plan to restrict harvest of lake trout to the public, even groups who accept the need to restrict harvest may reject that specific plan if they perceive that it does not meet all of their expectations and concerns. This response can be minimized if the groups have been involved in the planning. Public response can also be improved if the public is presented with not one plan, but alternative plans to compare and select from.

This process allows the public to understand the full range of values and risks presented by all alternatives. Public attention is focused on the management problem to be solved (e.g. restrict lake trout harvest) and on a range of solutions rather than a single plan. This has the added benefit of allowing the public to experience the same learning process as the manager in comparing solutions and understanding the problem. In using this strategy, however, care must be taken not to overwhelm the public with problems that are so large and complex as to prevent rational response (Weick 1984).

One of the unfortunate characteristics of public response is that citizens who are opposed to a plan often become involved in much larger numbers than those who support it (Peyton and Gigliotti 1985). To cope with this phenomenon, Great Lakes managers must select involvement procedures that encourage more participation by all groups.

Public surveys can be a useful means of obtaining representative input if they are properly designed. Stoffle et al. (1983, 1984) have shown the utility of surveying sport fishers to develop Lake Michigan fishery policies. Survey information is more reliable and useful if values, beliefs, and a range of other factors which may influence respondents' decisions are measured. Surveys dealing with specific issues should also assess how thoroughly the respondent has evaluated the issue (i.e. have all values and consequences been considered, is the information base adequate, etc.).

One threat to efforts to influence public beliefs, attitudes, or acceptance is a low credibility rating of the resource agency by the public (Dennis 1977; Peyton and Gigliotti 1985). There are two important components of the credibility factor. The public must view the agency as being competent to manage, and the public must trust the agency to represent the public's best interest. It is not difficult to envision various combinations of public perceptions of competence and trustworthiness and the implications those would have for implementing lake trout rehabilitation strategies. Agencies do not need to "sell out" their ecological values to gain credibility with the public, but they must sincerely reflect a wide range of values in their management.

If lake trout rehabilitation programs are to be publicly accepted, agencies will have to become more expert at issue management. A difficult aspect of this task will be for fisheries managers to develop, implement, and become skilled at strategies to deal with public value conflicts. Stoffle et al. (1984) discussed the difficulty of this task. They found that Wisconsin anglers objected strongly to any decrease in Wisconsin's coho stocking program and interpreted this to mean that they valued coho as their "bread and butter" species. Later, the same groups expressed similar concerns for lake trout when harvest restrictions were proposed for that species. The fishers were being consistent. They valued all salmonid species, but the value of most importance was that placed on a diversity of target species to support fishing activities over time and under varied conditions of species abundance.

Another difficult task involves finding ways to help the public develop skills in recognizing and, when necessary, reassigning priorities in difficult management issues. The methods for these tasks are not readily available. The processes will require that the public be involved over longer periods of time and have more opportunity to interact directly with other user groups. The methods may include interactive workshops (Doyle and Straus 1976) or adaptive management strategies (Holling 1978). Kearney (1984) observed that interaction between purse seine and weir herring fishers in the Bay of Fundy during a public involvement process improved their communications and mutual understanding.

Summary

Natural resource issues result when beliefs and/or values of individuals or groups are in conflict. The perceptions and value priorities of individuals armed with institutional means of disrupting resource management programs cannot be ignored. Further, they should not *be* ignored if our resource management is to represent all affected users.

A wide range of attitudes and factors determine public responses to management programs. Great Lakes resource agencies could better anticipate these factors and incorporate them in program planning if expertise were developed through inservice training and by creating positions for staff trained to deal with the public dimensions of management. Especially critical is the need for expertise to involve the public in resolving the difficult value conflicts in issues.

Great Lakes managers must invest in long-term programs to build rapport and credibility with the public, improve the public's understanding of and participation in the management process, and gain better understanding of public segments which are affected by Great Lakes management. The overall goal is to develop both agency and public capabilities to develop Great Lakes rehabilitation programs in the complex social environment of resource management.

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Biotic and Abiotic Determinants of Lake Whitefish (*Coregonus clupeaformis*) Recruitment in Northeastern Lake Michigan[1]

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Taylor, W. W., M. A. Smale, and M. H. Freeberg. 1987. Biotic and abiotic determinants of lake whitefish (*Coregonus clupeaformis*) recruitment in northeastern Lake Michigan. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 313–323.

Comparisons of lifetime average per capita reproductive rates (R_0) between stocks of lake whitefish (*Coregonus clupeaformis*) in Lake Michigan found higher estimates of R_0 for rapidly growing exploited stocks than for a commercially unexploited stock. Earlier maturation was the prime cause of this increase. Exploited stocks, however, were dependent on fewer age-classes for reproduction and had a greater potential for instability due to annual variation in recruitment. Overwinter whitefish egg survival in Grand Traverse Bay was nearly fourfold higher during a cold winter with prevalent ice than during the preceding mild, ice-free winter. However, the higher densities of larvae produced during the cold winter experienced greater mortality, with starvation the likely cause. Factors found to influence a stock–recruitment relationship developed for year-classes from 1958 to 1980 included spawning biomass, winter severity (ice-cover), and spring temperatures. Periods of abnormally high and low whitefish catch corresponded to periods in which cold or warm winters were more frequent, respectively. Harvest strategies that dampen naturally caused fluctuations in the spawning stock are recommended.

Des comparaisons entre les taux de reproduction (R_0) moyens par individu chez des stocks de grand corégone (*Coregonus clupeaformis*) du lac Michigan ont révélé des R_0 estimatifs plus élevés chez les stocks exploités à croissance rapide que chez un stock non exploité commercialement. La maturation précoce était la cause principale de cette augmentation. Toutefois, les stocks exploités sont tributaires de moins de classes d'âge pour la reproduction et montrent une instabilité potentielle plus élevée à cause de la variation annuelle du recrutement. La survie des oeufs de corégone après l'hiver dans la baie Grand Traverse était presque quatre fois plus élevée au cours d'un hiver froid où la glace était présente que pendant l'hiver doux précédent quand la surface de l'eau était libre de glace. Toutefois, les densités plus élevées de larves produites pendant l'hiver froid ont fait l'objet d'un taux plus élevé de mortalité, probablement à cause d'un manque de nourriture. Les facteurs qui influent sur la relation stock–recrutement élaborée pour les classes de 1958 à 1980 comprennent la biomasse reproductrice, la rigueur de l'hiver (couverture de glace) et les températures printanières. Les périodes de capture de corégone anormalement élevées et faibles correspondent respectivement aux périodes pendant lesquelles les hivers chauds ou froids étaient plus fréquents. On recommande des stratégies d'exploitation qui réduisent les fluctuations naturelles du stock reproducteur.

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Growth, survival, and recruitment are the three basic population processes which govern the yield from and persistence of exploited fish stocks. Of these, recruitment is the most difficult to analyze. Quantifying rates of replenishment requires assessing the reproductive capacity of the adult stock and analyzing survival and growth from the egg stage through the completion of the life cycle. Such cradle to the grave assessments of recruitment have been rarely, if ever, accomplished, and out of necessity, population dynamics have depended on certain theoretical assumptions about the recruitment process. In part because data on early life-history stages are scarce, recruitment is commonly assumed to be a function of adult dynamics. Survival and growth preceding recruitment are either assumed to be constant or to vary with the size of the adult stock in density-dependent fashion, as predicted by stock–recruitment theory (Ricker 1954; Beverton and Holt 1957).

Although it is often recognized that these expectations are assumptions of convenience rather than literal descriptions of the recruitment process, alternatives have not been thoroughly developed. The primary goal of our study of lake whitefish populations in northeastern Lake Michigan has been to analyze recruitment and how it is affected by both early life-history events and characteristics of the adult stocks. This paper is intended as a summary and a synthesis of the different segments

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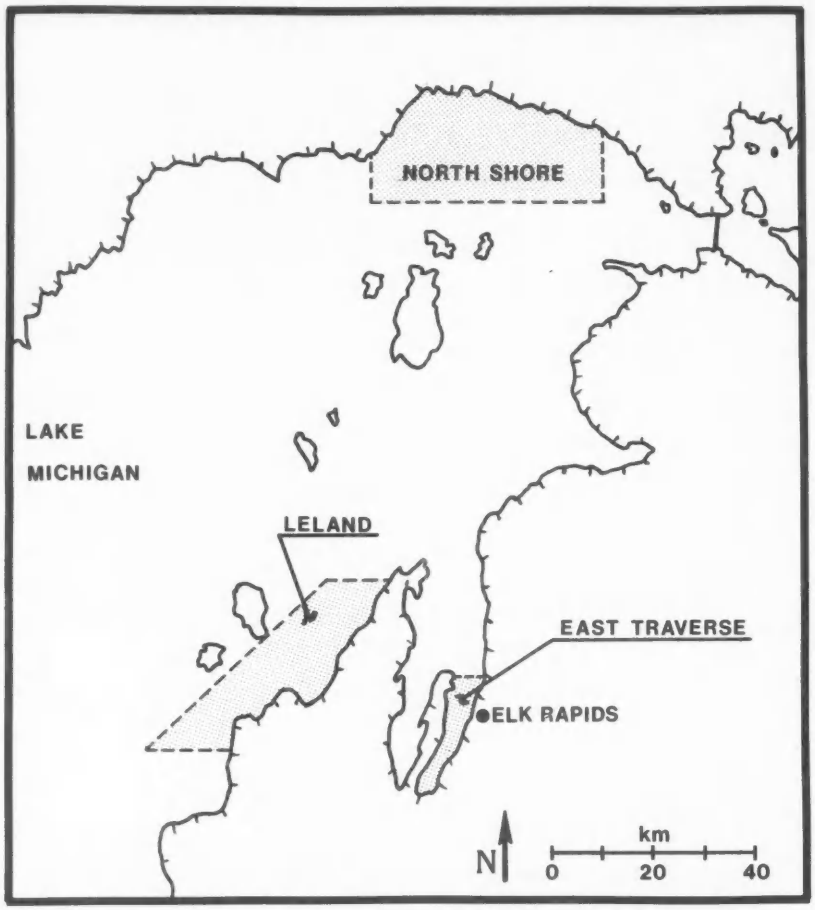

FIG. 1. Study area in northeastern Lake Michigan, including home range boundaries of the principal study populations.

of the study. More detailed descriptions of methods and results are available elsewhere (Taylor and Freeberg 1984; Jacobson and Taylor 1985; Scheerer and Taylor 1985; Freeberg 1985; Smale 1986) and only the broader perspectives are included here. Our intention is to test conventional concepts of recruitment and suggest alternatives when necessary.

Strong year-to-year variation in recruitment seems a common feature of exploited whitefish stocks, and several studies have investigated possible causes. Miller (1952) considered wind vectors following spawning to be the major factor determining recruitment in Alberta Lakes, while Christie (1963) and Lawler (1965) considered temperatures during incubation and larval development to be critical. But factors besides climate during the early life-history phase have also been considered important. Healey (1980) found that a surge of recruitment followed the onset of exploitation in previously unexploited lakes and considered some density-dependent mechanism as a likely explanation. Henderson et al. (1983) observed a significant decline in recruit per parent (R/P) ratios with increasing parental stock size, an observation which is consistent with stock–recruitment theory.

The turbulent history of Lake Michigan's whitefish fishery does not seem to support steady-state types of hypotheses about recruitment dynamics. Sharp peaks in yield circa 1932 and 1947 (Baldwin et al. 1979) contrast with periods of low yield, including the near extinction of populations prior to 1960. Yields since 1960 have increased steadily and were sustained at or near record levels for the decade preceding 1984. Neither Walter and Hoagman (1975) nor Hastreiter (1984) found any apparent relationship between the spawning stock size and either recruitment or R/P ratios in western Lake Michigan whitefish stocks. Explanations for changes in Lake Michigan yield have mostly focused on factors influencing adult dynamics such as exploitation rates and lamprey predation (Patriarche 1977). The influence of early life-history stages on these fluctuations has been largely unexamined.

Our study of recruitment dynamics consisted of three segments. In the first, factors influencing rates of adult egg production were compared amongst three stocks (Fig. 1): an intensely exploited North Shore stock, a moderately exploited Leland stock, and a commercially unexploited stock in the East Arm of Grand Traverse Bay (East Traverse stock). Current North Shore stock characteristics were also compared with those found in earlier studies (Caraway 1951; Piehler 1967;

Brown 1968) in order to evaluate within-stock dynamics as well as between-stock differences. Our objective was to determine whether factors such as growth compensation (Healey 1975) and early maturation (Jensen 1981) in exploited stocks were adequate to compensate for losses to the fishery.

A second phase of the study estimated survival rates of whitefish eggs and larvae from a spawning ground in the East Traverse area. Egg survival was related to overwinter climatic conditions, and the larval study was designed to test Cushing's (1982) Match–Mismatch Hypothesis. According to this hypothesis, starvation is the principal cause of larval mortality, and the degree of synchronicity between initiation of exogenous feeding by larvae and rapid increases in zooplankton production influences variation in survival. We modified the Match-Mismatch Hypothesis somewhat in that we expected that major pulses, or blooms, of zooplankton in the early spring would be largely temperature driven, whereas zooplankton blooms in ocean systems seem determined more by nutrient-laden upwellings. We hypothesized that mild spring temperatures would lead to early rapid increases in zooplankton dynamics and a better match in relative densities of larvae to zooplankton.

The early life-history segment was used to generate hypotheses about the recruitment process which were tested with North Shore stock–recruitment estimates developed for year- classes from 1958 to 1980. Relationships between R/P ratios and spawning biomass, a winter temperature index, and spring temperatures were the primary factors considered. Our intentions were to determine which variables would be most useful for predicting future recruitment and yield and to examine the relative importance of adult dynamics and early life-history dynamics in influencing recruitment variation.

Methods

Adult Whitefish Dynamics

Recruited whitefish dynamics at Leland and the North Shore were measured by a mark–recapture tagging program in conjunction with frequent trap-net catch sampling. Tags returned by cooperating commercial fishermen provided for estimates of home range, numerical abundance and biomass, and rates of fishing and nonfishing mortality. Catch samples, taken at least three times per year from October 1980 through 1984, provided estimates of age and length distributions, back-calculated growth, fecundity, and length and age schedules of maturation.

Both juvenile and adult whitefish were sampled from trawls made by the Michigan Department of Natural Resources (MDNR) in the East Traverse area during June 1983–85 and September 1984. Because there was no commercial fishing in this area, no estimates of home range or abundance were made. Estimates of back-calculated length and age and length schedules of maturation were made. Estimates of mortality were made from age structure data using catch curves. The estimate of prerecruited whitefish mortality from these samples was assumed to be the same for all areas.

Data on growth and maturation of North Shore whitefish for 1932 and 1966–67 were obtained from Piehler (1967) and Brown (1968). Age distributions for 1960–84 (with some missing years) were from these sources and Rybicki (1980[4]), MDNR unpublished catch data, and our study (Smale 1986). Most, but not all, whitefish were sampled from trap or pound nets.

Estimates of lifetime per capita reproductive output (R_0) were made from life-tables. For each stock, number of survivors from an initial cohort of 1000 age 0 female fish was estimated from mortality statistics. The number of survivors at each age was then multiplied by the percentage of mature females at that age. The average age-specific fecundity was calculated from estimates of the mean weight of mature females at each age and regressions of fecundity on weight. Summing the age-specific contributions provided the estimate of R_0.

Egg and Larval Whitefish Survival

Survival of whitefish eggs and larvae was measured in the East Traverse area because its relatively sheltered nature enabled more frequent sampling. Sampling was concentrated on and around a whitefish spawning ground less than 1 km south of the Elk Rapids Harbor during the falls of 1982–83 and springs of 1983–84.

An iron sled (Stauffer 1981) connected through flexible hose to a diaphragm pump and pulled alongside a boat across the bottom estimated relative densities of whitefish eggs. Egg sampling was conducted from mid-November into December and in late March until the first emerging larvae were found in April. Sampling was stratified across depth contours from 1.5 to 9 m, with towing speed and duration kept constant to standardize transects. The percent difference in depth-weighted average densities of eggs suctioned per transect between the November maximum and the density preceding emergence was the survival value used.

An ichthyoplankton trawl towed beside a boat sampled larval whitefish throughout April and May. A flowmeter inside the net measured water volumes passing through so that densities of larvae per cubic metre could be calculated. Inshore areas of the East Traverse coastline were subdivided into zones and grids so that sampling could be scheduled to counter patchiness of larval distributions. Length, weight, and stomach contents of captured larvae were measured. Larval mortality was calculated as the rate of change in weekly averaged densities of larvae.

Zooplankton densities were estimated with vertical hauls of Wisconsin plankton nets. Sampling was also scheduled on a stratified-by-zone, random grid within a zone basis, with samples taken over a 24-h period. Frequency distributions by taxonomic groups and by size-class were compared with distributions in the larval stomachs in order to evaluate electivity of their feeding behavior.

Stock–Recruitment Relationship

Estimates of North Shore spawning biomass developed from tag returns were used to calibrate a relationship between trap-net catch per unit effort (CPE) and spawning biomass:

$$\text{Spawning biomass (kg)} = \text{CPE (lb. per lift)} \times 3360.$$

This relationship was used to calculate spawning biomass from MDNR catch data. For 1958–64, trap-net effort in the area was too low for reliable population estimates. Regressions of trap-net CPE versus gillnet CPE calibrated the two gears against each other and biomass estimated from weighted means of the two gear types.

A modified cohort analysis procedure partitioned each annual biomass estimate amongst year-classes. Multiplying each biomass estimate by the percentage of the sampled catch in the

[4]R. W. Rybicki. 1980. Assessment of lake whitefish populations in northern Lake Michigan. MDNR Fish. Div. Unpubl. Rep. (PL 88-309): 27 p.

three most common age groups yielded a three-column-wide matrix of numbers of catchable fish from each cohort at three successive ages. Values were natural log transformed and the differences between the center column, or modal age, and the two adjacent columns were calculated. A 3-yr running mean of this difference between numbers at the modal age and adjacent ages was calculated, and then the mean difference for each year was added to either adjacent age. The procedure provided three independent estimates of numbers of whitefish in each year-class at its modal age in the catch. The mean of the three estimates was used as the index of recruitment, and analysis of variance was used to examine reliability of the means.

Based on results of the early life-history study, the North Shore stock–recruitment data were analyzed with respect to three factors: parental spawning stock size, winter severity and ice cover, and spring temperatures. Regressions of natural log transformed *R/P* ratios and spawning biomass estimates tested the stock–recruitment data for expected density dependence.

R/P ratios were regressed against a winter severity index which consisted of the average number of freezing degree days (FDD) accumulated through the third week of January at three northern Lake Michigan stations: Green Bay, Escanaba, and Traverse City. Data on ice formation dates in the North Shore area were insufficient to estimate freezeup dates directly. Therefore, FDD accumulations for the first half of the winter, which usually correlate well with ice formation and extent (Assel and Quinn 1979), were substituted for direct observations of freezeup dates.

Regressions of *R/P* ratios against a spring temperature index tested for increasing recruitment from warmer springs. The deviation in degrees (Celsius) from the long-term monthly mean summed for April and May and averaged for the same three Lake Michigan stations was used as the spring index.

Because early winter temperatures seemed to be an important factor in whitefish recruitment, we also examined the climatic record to determine whether winter severity was uniformly distributed across time or some patterned clumping of cold and mild winters was apparent. For the winters of 1897–1981, FDD accumulations through mid-January (Assel 1980a) were averaged for the three stations and the percent deviation from the mean was calculated. Winters that deviated from the mean by 25% or more were classified as either cold or mild, and by this standard close to half the winters were considered near normal and close to one quarter were mild and cold. A time-line plot of FDD deviations was examined for periods in which cold or mild early winters were unusually frequent.

Results

Adult Whitefish Dynamics

North Shore total instantaneous mortality rates were the highest of the three stocks (Z = 1.39-1.56), as was fishing mortality (F = 0.87). Mortality and exploitation rates at Leland were lower (Z = 0.73–0.89, F = 0.42) and the lowest for East Traverse whitefish (Z = 0.46, F assumed to be 0). In comparison with mortality estimates from other Lake Michigan stocks (Ebener and Copes 1985), North Shore whitefish could be considered intensely exploited and Leland whitefish moderately exploited. The East Traverse mortality estimate was similar to an estimate by Rybicki and Keller (1977) for a commercially unexploited stock in West Grand Traverse Bay.

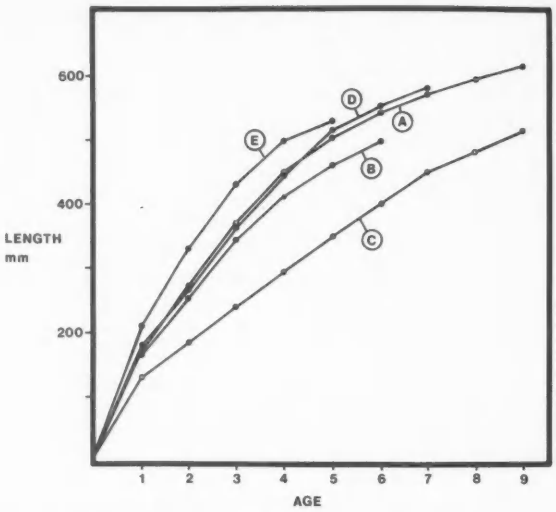

FIG. 2. Back-calculated lengths at age of whitefish in the Leland (A), North Shore (B), and East Traverse (C) areas during this study and North Shore, 1932 (D), and North Shore, 1966–67 (E).

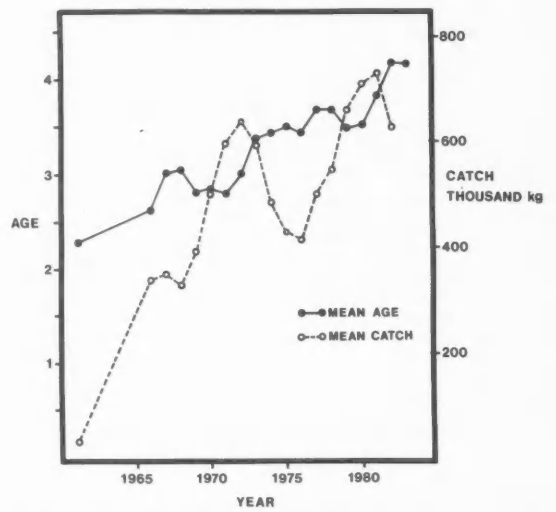

FIG. 3. Three-year running mean of the age of the North Shore catch in comparison with a 3-yr running mean of whitefish catch from District MM-3.

For prerecruited East Traverse whitefish, we estimated mortality to be Z = 0.50.

Back-calculated lengths at age (Fig. 2) varied considerably both between stocks and over time. From our study, current East Traverse growth was the slowest of all comparisons. Leland growth exceeded North Shore growth and the amount of difference increased with age. North Shore growth during 1966–67, a period when this stock was recovering from the population collapse of circa 1960, was the most rapid growth observed. During both 1932 and in this study, when catch records indicate that the North Shore stock was at normal to above-average densities, growth was relatively slower.

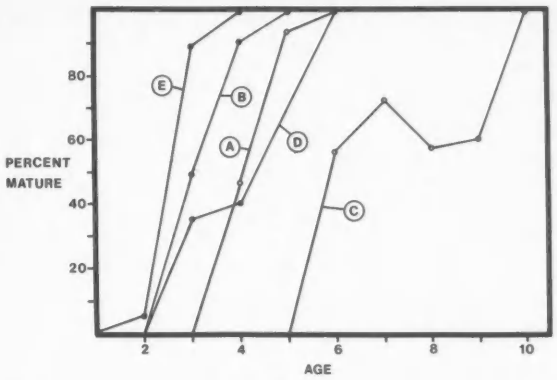

FIG. 4. Age schedules of female whitefish maturation in the Leland (A), North Shore (B), and East Traverse (C) areas during this study and North Shore, 1932 (D), and North Shore, 1966–67 (E).

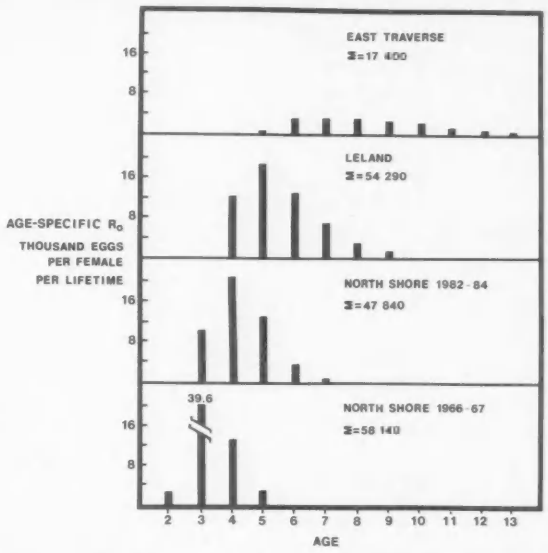

FIG. 5. Estimates of per capita lifetime egg production from cohorts of 1000 age 0 female whitefish in the principal study populations.

Since 1960, we found that the average age of the North Shore catch has tended to increase. A 3-yr running mean of age of the North Shore whitefish (Fig. 3) exhibited a nearly constant trend of increasing age, paralleled by an increase in the 3-yr running mean of catch from the area. We found no evidence that the average size of North Shore fish increased, and slopes of the right-hand limb of catch curve plots did not change significantly between 1960 and 1984. Apparently, as the North Shore stock grew in abundance between 1960 and 1984, growth decreased, mortality rates remained relatively constant, and the average fish in the catch became older but not noticeably larger.

Age schedules of female maturation (Fig. 4) also varied, with earlier maturation associated generally with more rapid growth. Earliest maturation was found for 1966–67 North Shore fish, with some mature females found as young as age 2. East Traverse maturation was most delayed, with immature females found up to age 9. We also found variation in the length at which maturation occurred: East Traverse and Leland females matured at both a larger size and later age than North Shore females. But within the North Shore stock, maturity occurred at later ages in both 1932 and this study, when growth was relatively slow.

R_0 estimates were considerably different amongst the stocks (Fig. 5). Highest rates, estimated for the 1966–67 North Shore population, were over threefold greater than the lowest estimate for the unexploited East Traverse stock. Current Leland and North Shore R_0 estimates were similar, with increased R_0 at Leland due to lower mortality and greater growth nearly cancelled out by the effect of exploitation of Leland fish beginning at a size below maturity. Delayed maturity was mostly responsible for the low East Traverse R_0. The extended juvenile phase resulted in fewer members of the original cohort surviving to reproduce, even though juvenile mortality rates were assumed constant for all estimates.

We solved the life-tables for a survival rate from egg to age 0 which would result in zero population growth for East Traverse fish (2000 survivors per 1.74 million eggs) and substituted this rate into Leland and North Shore life-tables. Such a rate resulted in 22–25% per year population increases for the two exploited stocks.

A second principal difference between life tables was that higher R_0 values were associated with increased dependency on fewer ages for reproductive contributions. The maximum contribution by any single East Traverse age-class was 18%, for Leland 34%, current North Shore 44%, and 1966–67 North Shore 68%. Simulating variable rates of survival from egg to age 0 resulted in much greater variation in R_0 values for the exploited stocks than for East Traverse simulations. Increases in R_0 seemed to occur at the cost of potentially greater population instability.

In interpreting results from these life-tables, a distinction between per capita rates of reproduction and total population fecundity must be made. If reducing the overall population density is necessary to accelerate growth and maturation, the result would be a smaller standing stock reproducing at a higher per capita rate. Whether total population fecundity increases, decreases, or remains constant when stocks are reduced below carrying capacity by exploitation or other events was not determinable with the data available.

Egg Survival

Estimated overwinter egg survival on the East Traverse spawning ground increased from 1.4% during 1982–83 to 5.5% in 1983–84, an almost fourfold increase. Initial egg densities were the same in both years, with densities greatest at 1.5 m depth and least at 9 m. No surviving eggs were found beyond 1.5 m in 1983, and survival decreased with increasing depth in 1984 also.

The two winters were distinctly different in character. Temperatures during 1982–83 were extremely mild, and FDD accumulations at Traverse City that year were the second lowest of this century. Grand Traverse Bay was virtually ice-free all winter. The 1983–84 winter was colder than normal, with mid-winter FDD accumulations exceeding 92% of the winters since 1897. Inshore ice cover developed in early January and the East Arm was frozen over from mid-January through March. During the ice-free winter, spawning grounds were exposed to wind and wave action throughout the winter, and bottom scouring and substrate movement appeared substantial. The presence of ice the following year seemed to reduce these

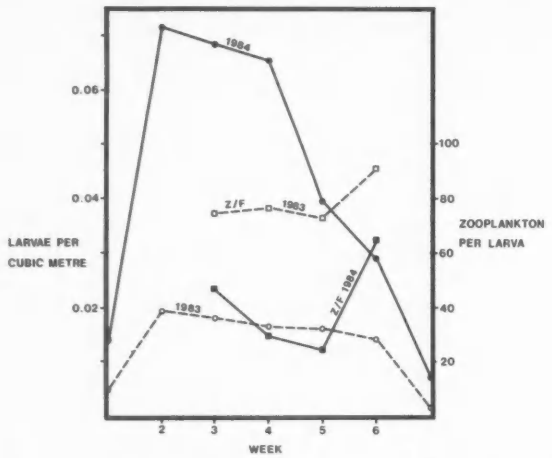

FIG. 6. Larval whitefish densities in the East Arm of Grand Traverse Bay during 1983–84 in comparison with zooplankton per larva ratios.

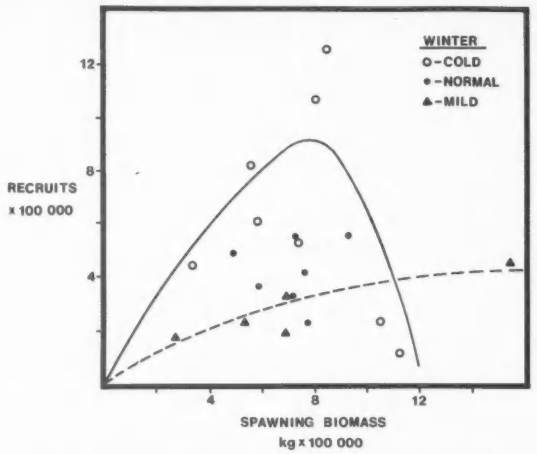

FIG. 7. North Shore stock–recruitment relationship for the year-classes from 1958 to 1980. Solid curve is calculated for the eight coldest winters and the broken curve for the five mildest winters.

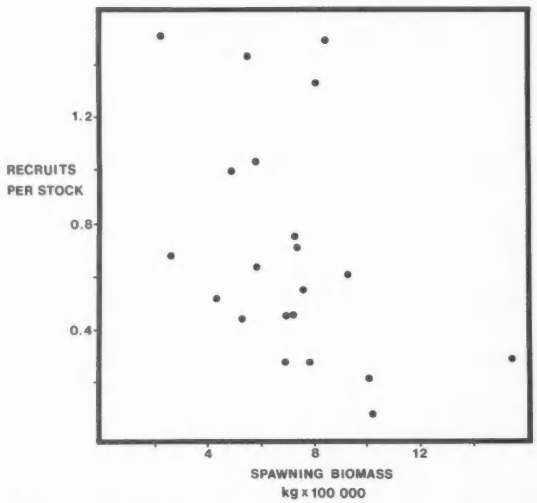

FIG. 8. Recruits per unit of spawning biomass in relation to stock spawning biomass.

factors considerably, as evidenced by extensive periphyton mats which were found on the bottom after the second winter but not the first. Sturdy fry traps anchored to the bottom were either crushed or swept away during the ice-free year of 1982–83. The higher egg mortality in 1982–83 was thus a function of mechanical destruction of the eggs and shifting of the substrate, while this factor was diminished the following year by the blanketing effect of ice formation.

Larval Survival

Initial peak larval densities following the ice-bound winter were 3.7 times higher than in the preceding year. However, this larger larval cohort experienced greater mortality during the 6 wk between emergence and migration to deeper water, reducing the difference in year-class strength to 2.1-fold. Larval survival during 1983 was estimated at 73% for the 6-wk period, with little variation in mortality noted from week to week. Survival during 1984 was 41%, with a sharp increase in mortality during the fifth week.

Larval whitefish consumed intermediate-sized copepod and copepodite zooplankton with a marked degree of electivity, virtually ignoring the more numerous but smaller zooplankton. Laboratory feeding trials (Taylor and Freeberg 1984) found that larval mortality increased rapidly when zooplankton per fish (Z/F) ratios fell below 32. During 1983, ratios of zooplankton in utilized size-classes per larva never fell below 40, and survival remained relatively high and constant (Fig. 6). In 1984, larval densities were higher and Z/F ratios correspondingly lower. The steepest larval mortality occurred during the fifth week, when Z/F ratios fell to 26, their lowest value, and larval growth became negative. The correspondence between differences in both annual and weekly mortality rates and differences in Z/F ratios indicated that starvation was the likely cause of the increased mortality observed in 1984.

Both springs were similar in character, with April and May temperatures at Traverse City below average. Rapid increases in zooplankton densities occurred after the sixth week, about the time larvae began to shift to nonzooplankton food sources and migrate to deeper water. Because of the lack of contrast between the two springs, we were unable to test for shifts in zooplankton dynamics due to spring temperature effects. Nonetheless, zooplankton blooms in both relatively cool years occurred too late to have a major positive impact on larval growth and survival.

Stock–Recruitment Analysis

Variation in recruitment at any particular stock size was quite large (Fig. 7). The five smallest and largest stocks produced only small to average recruitments. Intermediate spawning stocks produced the greatest variation in year-classes, with about a 12-fold maximum difference occurring in recruitment from similar stocks.

As expected from stock-recruitment theory, R/P ratios tended to decrease with increasing stock size (Fig. 8), but with a great deal of scatter. The correlation between $\log_e$ (R/P) and

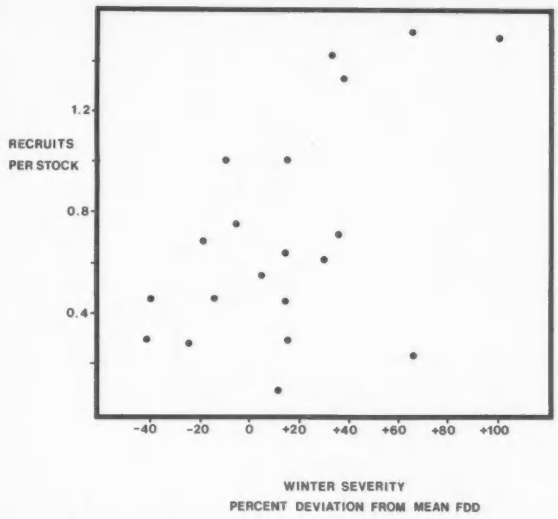

FIG. 9. Recruits per unit of spawning biomass in relation to percent deviation from the mean accumulation of freezing degree day through the third week of January.

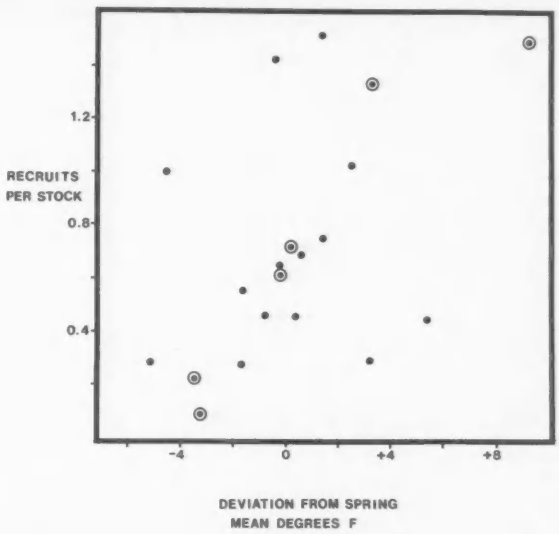

FIG. 10. Recruits per unit of spawning biomass in relation to deviation from the mean April–May temperatures. Circled points identify years of expected high larval densities (see text for explanation).

$\log_e (P)$ was significant ($r = -0.52$, $p < 0.05$), but the resulting stock–recruitment relationship explained only 1.4% of the total variation in recruitment when non-log-transformed values were considered. Although density dependence was apparently a factor influencing recruitment, recruitment could not be predicted with meaningful reliability from stock size alone.

The correlation ($r = 0.50$, $p < 0.05$) between the percent deviation of FDD's accumulated through mid-January from the long-term mean and *R/P* ratios was also significant (Fig. 9). Large recruitments and high *R/P* ratios occurred during cold winters, and milder winters produced below-average ratios and small recruitments. But there were also exceptions: not all cold winters resulted in high *R/P* ratios, and not all low ratios resulted from mild winters. This set of observations indicated that although winter conditions influenced recruitment, winter was also definitely not the only influential factor. Stock–recruitment curves calculated separately for the eight coldest winters and five mildest winters of the 20 yr (Fig. 7) were distinctly different. During mild winters, recruitment increased slowly and in linear fashion with stock size. In cold winters, a strongly dome-shaped relationship, symptomatic of density dependence, occurred. Smaller year-classes resulted from cold winters only when spawning stocks were above average.

Spring temperature deviations were less strongly correlated with *R/P* ratios ($r = 0.39$, $p < 0.10$) when considered alone. A plot of the relationship (Fig. 10) showed a general increase in *R/P* ratios for warmer springs, but with some very definite exceptions. Those exceptions, however, were years in which spawning stocks were low and/or the winter was relatively mild. When we isolated 6 yr in which winters were colder than normal and spawning stocks above average (circled points in Fig. 10), the relationship became less ambiguous: mild springs produced very high *R/P* ratios and cold springs produced very low ratios. If spring temperatures were an influence, they interacted with egg deposition and egg survival in such a manner that spring conditions became increasingly critical with increasing larval densities. This expectation is consistent with our early life-history findings, which indicated that if larval densities are low enough, variation in zooplankton density is irrelevant because *Z/F* ratios will still be above critical levels.

The distribution pattern we found for early winter temperatures since 1897 was clumped rather than uniform. Unusually cold and mild winters (greater or less than 25% deviation from the norm) between 1897 and 1920 were both more frequent than since 1920, but each type occurred with nearly equal frequency (Fig. 11). From 1921 through 1930, four cold but only one mild winter occurred. Between 1931 and 1958, only two cold winters occurred but nine winters were unusually warm. From 1959 through 1984, 10 of the 26 winters were cold, while only three were mild. The period included in the stock–recruitment analysis (1958–80) was exceptionally cold in comparison with the twentieth century norm, skewing the analysis toward colder years. Other investigators have noted that the period circa 1930–60 was abnormally warm, but temperatures since 1960 were colder (Eichenlaub 1979; Ayers 1965; Assel 1980b).

There was a strong correspondence between the distribution of FDD accumulations and the historic record of Lake Michigan whitefish yield (Fig. 11). A high frequency of cold winters during the 1920's was followed by peak yields just after 1930. The second peak in yield circa 1947 was due to an exceptionally large 1943 year-class, produced during one of the two cold winters between 1931 and 1958. Van Oosten (1944) commented on the below-average water temperature and above-average ice cover that fall and winter. Excepting the 1943 year-class, the trend in yield was an almost continual decline from 1932 until 1960, with yield minima circa 1940 and 1960 both following extended periods when cold winters were absent. The reversal in the relative frequency of cold to mild winters which began with the winter of 1959 was associated with a reversal in the trend of decreasing yield. Since 1960, yields have climbed in most years up to record levels after 1980, which followed a series of extremely cold winters from 1977 through 1979.

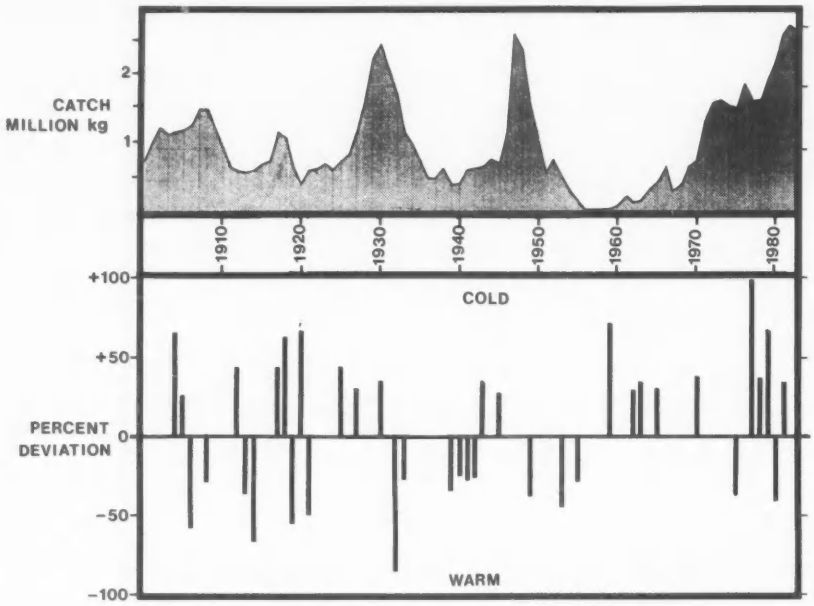

FIG. 11. Comparison between Lake Michigan whitefish catch between 1900 and 1982 and the distribution of unusually cold and mild winters during the period. Unusual winters are those in which the accumulation of freezing degree days by mid-January deviates by more than 25% from the mean.

Discussion

The classical equilibrium and steady-state kinds of models commonly used to assess dynamics of exploited fish stocks are, we suggest, wholly inappropriate and misleading for Lake Michigan whitefish stocks. Annual variation in recruitment is substantial, and the default assumptions that early life survival is constant or influenced only by egg deposition from the adult stocks are clearly contradicted. Our viewpoint is in some respects pessimistic, in that we believe the ability to predict and control the fate of these stocks through dynamics of the fishery is limited. Natural factors, in particular climatic conditions, have a relatively powerful impact on the stocks, especially when these conditions occur in a clumped pattern. But we are also optimistic in that we regard these nonequilibrium dynamics as potentially predictable and manageable, when recruitment variation is understood and incorporated in yield models. Jensen's (1981) expectation that whitefish compensate for exploitation through accelerated growth and early maturation seems valid, but with qualifications. Density dependence influenced growth in two types of comparisons: between an unexploited stock and exploited stocks and within the same stock at two different densities. Growth in the commercially unexploited stock in Munising Bay of Lake Superior (Edsall 1960) was also much slower than in nearby exploited stocks (Dryer 1963), indicating that our results were not atypical. Earlier maturation was associated, for the most part, with accelerated growth, but the larger size at which maturation was attained in populations such as Leland also influenced R_0 estimates. Other population-specific characteristics such as length-weight and fecundity-weight relationships varied enough that reproductive statistics would best be analyzed stock by stock.

Even though growth varied principally with population density, population density varied in some cases independently of exploitation. The expansion of the North Shore stock between 1960 and 1981, for example, occurred despite high rates of exploitation throughout the period. The margin of what Healey (1975) termed the compensatory reserve cannot be predicted from mortality rates alone. Unusually frequent years favorable to recruitment seemed to produce an increase in the density of North Shore whitefish along with slower growth, delayed maturation, increased age, and a lower per capita production of eggs.

Our finding that R_0 estimates were higher in exploited stocks than in the unexploited stock is equivalent to the common finding that populations reduced below their carrying capacity by exploitation or other factors exhibit an increased capacity to expand back to their original density. Ideally, in unexploited populations of whitefish, we would expect a high proportion of the population to consist of juveniles. When growth is slow, fish remain juveniles for a longer period and juveniles would tend to accumulate. Exploiting this hypothetical stock would eventually reduce population density and accelerate growth, increasing the number of juveniles which survive to become adults. We would then expect to find a smaller proportion of the population consisting of juveniles, and the increasing numbers of new adults would offset those removed by the fishery. The classical expectation that exploitation produces a population in which reproduction is gamete limited and recruitment and stock size decrease in a downward spiral seems neither appropriate nor necessary in explaining population collapses.

If survival through the egg and larval stages were equal amongst populations and constant over time, we would expect the Leland and North Shore stocks either to increase more rapidly or decline less slowly than the East Traverse stock. But

the second difference between stocks, the varying dependency on fewer ages for reproduction, becomes important when the nonequilibrium dynamics are considered. Recruitment of a large year-class would result in a much greater increase in the spawning capacity of the North Shore stock than of the East Traverse stock. However, at East Traverse, the impact of a large year-class would extend over a greater span of years. Year-class failures would also have a much greater and more concentrated effect on North Shore reproductive capacity, and two successive poor year-classes could reduce the North Shore stock to a small fraction of its original abundance.

Although natural disasters during the early life history are apparently a prerequisite to rapid population declines, exploitation decreases the number of reproducing age-classes and is a second necessary condition for population failures to occur. Pessimistic forecasts about the immediate fate of the North Shore stock which were based on the high rates of exploitation (Patriarche 1977) were contrary to the actual behavior of this stock. Rather than decline, it actually increased due to the favorable effects on recruitment of recent harsh winters. The most important effect of exploitation on reproductive dynamics is not a direct reduction in gamete production. Rather, exploitation acts to reduce the buffering capacity of the population against natural variation in recruitment. This decreased buffering and increased potential instability is simply not analyzable from a steady-state perspective. Given that significant natural recruitment variation occurs, we would suggest an indeterminancy principle for stock dynamics: the more intensely a stock is exploited, the less accurate steady-state models become for describing and predicting population behavior.

The margin of compensatory reserve available within a stock provides a second type of buffering effect. In populations where growth is well below its potential maximum, we would expect poor year-classes to result in reduced juvenile densities, accelerated growth, and compensatory increases in R_0. Reproductive rates for whitefish stocks are apparently adjustable rather than fixed, and the slower rates of unexploited stocks imply that they function with a greater potential range of adjustment to variations in density.

Growth variation also influenced North Shore recruitment, but changes were gradual rather than strongly variable from year to year. The mean North Shore age at recruitment increased from 2.9 to 4.3 yr between 1960 and 1984. Given a constant juvenile mortality rate of $Z = 0.50$, this 1.4-yr increase would result in 51% fewer recruits from equal-sized juvenile cohorts. This mechanism is largely density dependent and is consistent with stock–recruitment in that R/P ratios would decline with increasingly dense stocks. Variations in growth amongst year-classes were present in our study, but were small in comparison with the total range of growth changes found for the North Shore stock.

Year-class formation for Lake Michigan whitefish is a three-step process: egg deposition, which is largely a function of spawning biomass; egg survival, which varies with the extent to which ice formation suppresses mechanical destruction of the eggs; and larval survival, which varies with Z/F ratios. Larval densities are a product of two factors: egg deposition and ice formation, and different combinations of stock size and winter severity can result in equal densities of larvae. If zooplankton densities were constant from year to year, larval survival would be strictly density dependent and the relationship could be analyzed as a "larvae–recruitment" relationship rather than a stock–recruitment function. However, both larval and zooplankton densities vary, and the Z/F ratio is a function of spring temperatures as well as larval density. The combination of a mild winter followed by a cold spring could result in high larval survival rates when Z/F ratios remain above critical levels because of low larval densities. Strong year-classes, such as the 1977 cohort, result when cold winters produce high egg survival and large numbers of larvae, and rapid spring warming induces high zooplankton production and therefore good larval survival. Poor year-classes occur from several combinations of factors: very small stocks and inadequate egg deposition, delayed ice formation and poor egg survival, or very high larval densities, cold springs, and poor survival.

Even though we found a broad range of recruitments from equivalent stocks, the influence of stock size on recruitment is not negligible. The maximum variation found at a given stock size was 12-fold; thus, the extent of variation is limited but broadly so. Very small stocks, even under ideal conditions for recruitment, were capable of producing moderate year-classes at best. In 1959, for example, the exceptionally cold winter and following mild spring resulted in an extremely high R/P ratio but only a modest recruitment due to the low initial egg deposition. Density dependence, the basis of stock–recruitment theory, does seem to influence recruitment. The largest stocks produced, at most, average recruitments, and R/P ratios tended to decline with increasing stock size. The four largest spawning stocks in the study by Henderson et al. (1983) produced both the lowest R/P ratios and the smallest year-classes, which also suggests strongly negative consequences of excessive larval densities. The larval survival segment of our study found that zooplankton densities can be limiting to survival. Both year-to-year and weekly variations in mortality coincided with Z/F ratios. In some respects, our study is consistent with stock-recruitment theory in that density is an important determinant of survival. But we would qualify stock–recruitment theory in two respects: larval abundance is not just a function of stock size, and the carrying capacity to which density is relative is also variable.

Evidence for a strong influence of early winter conditions on recruitment was threefold: the large difference in egg survival between the two winters, the strong shift in the North Shore stock–recruitment relationship due to different types of winters, and the correspondence between episodes of cold and mild winters and periods of high and low yields. The power of this factor in influencing larval densities is considerable. The measured increase in egg survival from 1.4 to 5.5% is equivalent to a 3.9-fold increase in egg deposition. Even though the highest R/P ratios for the North Shore year-classes occurred during the coldest winters, it is necessary to explain why some very cold winters produced poor to average recruitments and low R/P ratios. Large spawning stocks and cool springs were common factors in such cases, and very poor larval survival due to densities far in excess of a reduced carrying capacity is an explanation consistent with the larval study.

The variable we used to describe critical winter conditions, FDD accumulations, is a less than ideal index of the factor we consider important to egg survival: mechanical stress in the substrate. Besides air temperatures, ice formation is secondarily influenced by wind vectors and fall heat budgets. More direct observations of conditions on the spawning grounds, perhaps with satellite photographs, would be useful in predicting survival. We also chose to ignore, for the time being, the possible effects of storms and winds between spawning and freezeup as determinants of egg survival. We suspect that this

factor is important in years when storms are abnormally frequent or scarce. But our data were insufficient to calibrate egg survival against winds of varying intensity, duration, and direction. Year-classes in our study area have largely been in phase during recent years, but they have not been in phase with year-classes on the western side of Lake Michigan (Ebener and Copes 1985). Lee shore/windward shore differences could explain this difference.

Data to support the contention that spring temperatures are influential to recruitment are less conclusive, but the evidence available does not contradict this hypothesis. In the larval study, densities of zooplankton were not markedly different in the two years, but neither were climatic characteristics. Spring temperature deviations were only weakly correlated with North Shore *R/P* ratios, but testing for temperature effects independently of the other two factors, stock size and winter severity, is not entirely a valid assessment. The conclusion that if spring temperatures are important, they are not important in years of low larval density is supported by both the larval study and the stock–recruitment analysis. Years in which *R/P* ratios did not correlate with spring temperatures had either mild winters or small spawning stocks. Conversely, the three largest year-classes were from milder than normal springs. In terms of stock–recruitment theory, we would postulate that there is not just one larvae-recruitment curve, but a series of relationships ranging from a steeply domed, highly density-dependent curve in cold springs to a broader dome with a higher peak in warm springs.

Management of populations exhibiting significant variations in recruitment is a difficult, challenging task. Our data clearly show that stock dynamics can only be interpreted and forecasted through an understanding of the interplay of abiotic and biotic factors at all life stages. In Great Lakes whitefish populations, these interactions have resulted in a large variation in recruitment and yield over time. We believe that this variability is predictable and can be dampened through proper regulation of the fishery regulations which are adaptive (Walter 1986) and account for biotic and abiotic control of the growth and recruitment process.

In lake whitefish, diminished equilibrium dynamics are not the principal function of exploitation. Instead, exploitation acts to accelerate disequilibrium processes in the stocks by reducing their capacity to buffer and compensate for environmental variation. To counteract this loss, management strategies which enhance stability of the spawning stocks would be ideal; strategies which contribute to increasing variation would be counterproductive. Maximizing spawning biomass would not be a desirable goal, given the likelihood that larger egg depositions decrease the probability of larger recruitments. Maintaining spawning stocks within a range of moderate sizes and avoiding a reduction in biomass to the point where reproduction becomes gamete limited would both seem desirable.

Adaptive management techniques which readily respond to the recruitment process are suggested as the appropriate management strategy for Great Lake whitefish. This mode of management would ensure conservative strategies to be employed in years of poor recruitment conditions preventing the catastrophic collapse noted in the 1950's and opportunistic policies implemented when atypically favorable recruitment occurs, as in the 1970's.

Acknowledgments

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An Indirect Rapid Methods Approach to Assessment

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Strategies and tactics are explored for increasing the usefulness of assessment information obtainable under manpower and budget restrictions. A concept of indirect rapid assessment is gradually emerging based on a collection of rapid methods of varying degrees of accuracy, sophistication, and data requirements. These tactics involve the use of statistics which are functionally related to parameters of interest. Stock composition, growth, mortality, population size, intrinsic rate of increase, and stock production may be efficiently estimated with these methods. Short-term forecasting is also possible. Tactics include group testing, correcting biased estimates, use of comparative studies, using length as a substitute for age, and remote sensing type assessments.

On exploite les stratégies et tactiques afin d'augmenter l'utilité des résultats d'évaluation qu'on peut obtenir sous des restrictions budgétaires et manuelles. Un concepte d'évaluation indirecte et rapide se développe à partir d'un ensemble de méthodes rapides dont le degré d'exactitude ainsi que les exigences de données varient. Ces tactiques engagent l'emploi de statistiques qui sont liées de façon fonctionnelle aux paramètres en question. Par ces méthodes on peut ainsi estimer de façon efficace la composition de stock, la croissance, la mortalité, la taille de la population, le taux intrinsique de croissance et la production de stock. On peut également faire des prévisions à terme court. Les tactiques comprennent les examens en groupe, la correction des estimateurs biaisés, l'emploi d'études comparatoires, la substitution de l'âge par la longueur ainsi que les données reçues par satelites et avions.

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Fishery biologists around the world must face the realities of assessing fisheries under budget and manpower constraints. In this paper, we examine indirect rapid assessment techniques which involve the use of easily obtained statistics that are functionally related to the assessment parameters of ultimate concern. We attempt to develop a general concept of indirect rapid assessment methodology by cataloging and reviewing diverse approaches which can be used by fishery biologists. These approaches include group testing, sampling with two measuring devices of different accuracy, using comparative studies, etc. Several approaches presented are new to fishery biology.

Historically, there have been a number of rapid assessment techniques available but these techniques were generally quite crude. Hence, the term "quick and dirty" was an accurate description in many cases. Many of these techniques have evolved into sophisticated methods.

The variety of strategies available to fishery scientists for dealing with budget and manpower limitations can be contrasted by considering a simple example: suppose one wants to estimate the natural mortality rate in an unexploited fish stock. A traditional approach is catch curve analysis. The technologically oriented fishery biologist may try to develop a faster, automated system for preparing hard parts for examination, or to automate the process of measuring ring radii with a digitizer pad. The statistically oriented biologist might try to determine the minimum sample size which will provide the needed information and might advocate a sequential approach to collecting data. Both types of biologist may combine their general approach with the use of an age–length key. The key, which substitutes easily collected length frequency data for some of the harder to obtain age data, was one of the first "indirect rapid" techniques to be developed. The indirect assessment biologist has other options: age just enough fish to be confident of finding the oldest age in the sample and utilize the relationship between longevity and

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mortality rate to estimate mortality; or age enough fish to estimate the growth parameters — and then estimate the mortality rate from the mean size in the population or from the relationship between growth parameters and mortality rate. These ideas and a variety of other approaches to assessment are explored in the following sections.

Group Testing

Suppose one wants to estimate the prevalence of a certain trait which is known to be rare. Then most units (e.g. animals) tested will show negative results, i.e. the absence of the trait. In this case, one may wish to look for a method of testing randomly formed groups of units.

For example, the parasitic copepod *Mytilicola intestinalis* occurs in the blue mussel *Mytilus edulis* throughout much of western Europe's coastal waters. Detecting the presence of the parasite by dissection is a slow and tedious procedure. Dare (1977) devised a rapid procedure based on treating batches of mussels with the proteolytic enzyme papain and then sifting through the residue under a low-power dissecting microscope to detect the undigested chitinous exoskeletons of *Mytilicola*. If mussels are randomly assigned to jars, then the number of jars showing the parasite must be related to the proportion of animals having the parasite.

The maximum likelihood estimator is given by

$$(1)\quad \hat{p} = 1 - \left(1 - \frac{X}{n}\right)^{1/k}$$

with asymptotic variance given by

$$(2)\quad V(\hat{p}) = (1 - q^k)q^{2-k}/nk^2$$

where $\hat{p}$ is the estimate of the proportion p of animals with the trait (parasite), $q = 1 - p$, X is the number of groups (jars) showing the trait, n is the number of groups, and k is the number of units per group (mussels per jar) (Gibbs and Gower 1960; Thompson 1962; Sobel and Elashoff 1975).

Suppose one only has time to do 50 tests and one wishes to estimate the proportion of animals that are infected when the infection rate is actually 4%. If animals are tested in groups of one (i.e. 50 animals are individually tested), the standard error of the estimate would be $\sqrt{p(1-p)/n} = \sqrt{(0.04)(0.96)/50} = 0.03$. If animals are tested in groups of two (i.e. 100 animals tested in 50 tests), the standard error would be (approximately) 0.02.

Thus, it is clear that when dealing with rare traits, increased efficiency over ordinary binomial testing (one animal per test) can be obtained by testing randomly formed groups. This gain in efficiency can make it possible for a researcher to conduct larger, more detailed studies, e.g. of the importance of spatial or temporal pattern.

Care must be taken, however, not to place too many units in a group. Otherwise, all tests may turn out positive which leads to a maximum likelihood estimate of 1.0 even though the actual proportion could be much less. The statistical theory behind group testing has been described by Hoenig (1981) and Loyer (1983).

For group testing to be worthwhile, it must be almost as easy to test a group as it is to test an individual. This generally means it must be possible to physically combine tissue or body waste samples. For example, in testing for whirling spore disease (*Myxosoma*), one could macerate several fish heads simultaneously in a blender and stain the spores in the pooled sample provided there is no loss in sensitivity caused by dilution with uninfected fish (Markiw and Wolf 1980). A procedure that involves histological examination of tissues would not be suitable for group testing as there is no way to scan several samples simultaneously under a microscope. A variety of applications are suggested in Table 1. To date, only Worlund and Taylor (1984) appear to have used group testing for fisheries work.

An extension of group testing is the estimation of multinomial proportions. Suppose there are three stocks or species whose spatial and temporal distributions need delineation. A simple procedure would be to process samples by electrophoresis from a large number of individuals from various areas, depths, habitats, and times. But consider the results of testing groups of two fish at a time. If the banding pattern of each taxon has at least one unique identifier, then there is no loss of information in testing groups of two. Thus, if just pattern B is seen, both animals must have been from stock B; if A and B are seen, one must have been from A and the other from B.

If group size is greater than two, the results become equivocal. For example, if group size is three and A and B are seen, there could have been two from stock A and one from B or one from A and two from B. It then becomes a statistical problem to estimate the stock proportions in a sample. Unfortunately, little theoretical work appears to have been done in this area. As processing at sea becomes more common it may become more imperative to develop rapid biochemical tests for identifying processed foods so that landing statistics can be compiled on shore. Biochemical means of identifying taxa are discussed in Suzuki et al. (1981) and Ekaratne et al. (1982).

Group testing procedures can also be developed for other multivariate studies. For example, suppose one wants to study the co-occurrence of two rare parasites in a host species. The usual procedure is to record the presence/absence of the parasites in each individual host. However, by pooling samples of blood, feces, etc., one could test in groups. Estimation of the prevalence rates for each parasite proceeds as for the univariate case (i.e. ignoring the information on the "other" parasite). However, it now becomes of interest to estimate and test the degree of association of the parasites (Hoenig and Lawing 1984).

In general group testing situations, less information is obtained per item (animal) tested than if the items were tested individually. However, for suitably chosen group sizes, the information gained per test can be considerably higher than when units are tested in groups of size one.

Further developments include estimation when retesting is possible (Sobel and Elashoff 1975), group testing with a continuous variable (Sobel and Tong 1976), and development of a general theory of composite sampling (Rohde 1979).

Correcting Error-Prone (Biased) Surveys

Suppose one has the choice of using an inexpensive but error-prone technique to estimate the relative abundance of certain traits or using a time-consuming or high-priced technique which is (more) exact. The logical choice of a single technique would depend on a number of factors and thus is not easily specified. However, it is possible to use the inexpensive technique to conduct an extensive survey and use both techniques on a small sample to derive correction factors (Hoenig and Heisey 1984, 1986, 1987).

As a simple example, consider a survey to estimate the stock

TABLE 1. Biological applications of group testing (after Hoenig 1981).

Detect	In	By	Reference
Helminth eggs	Feces	Physical separation	Weller and Dammin 1945
Whirling disease spores	Fish heads	Maceration and flotation	Markiw and Wolf 1980
Kidney disease bacteria	Salmonid kidneys	Fluorescent antibody	Bullock and Stuckey 1975
Parasitic copepods	Bivalve mollusks	Enzyme digestion	Dare 1977
Ticks, fleas, mites	Mammal pelts	Chemical digestion	Zumpt 1961
Protozoa, bacteria, fungi, etc.	Blood, urine, feces, sputum, mucus	Microbial culture	
Virus	Pancreas, kidney, liver, etc.	Culture; antiserum neutralization	Cone and Moore 1981
Identify species	Mollusks and crustaceans	Latex agglutination test	Suzuki et al. 1981
Proteins (indicative of race or genetic makeup)	Muscle or other tissue	Electrophoresis	
Plant viruses	Insect vectors	Multiple transfer of insects to plants	Gibbs and Gower 1960

composition in a fishery exploiting two stocks. The inexpensive, rapid technique might consist of assigning fish to stocks on the basis of meristic or morphometric characteristics. A more precise but expensive technique would be to use electrophoretic results to classify animals.

The extensive survey using the error-prone technique results in a vector of estimates denoted by

$$E = \begin{bmatrix} e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} \text{proportion stock X} \\ \text{proportion stock Y} \end{bmatrix}$$

The use of both techniques on a sample, *not necessarily random*, results in correction data of the form

	Classified as:		
Actually	stock X	stock Y	sum
Stock X	a	b	m
Stock Y	c	d	n
sum	r	s	N

Placing the tabled values in a matrix and dividing by the corresponding row totals gives the matrix

$$(3)\quad P = \begin{bmatrix} a/m & b/m \\ c/n & d/n \end{bmatrix} = \begin{bmatrix} p_{11} & p_{12} \\ p_{21} & p_{22} \end{bmatrix}$$

which estimates the probabilities of classification. It follows, then, deterministically, that the actual stock composition, denoted by the vector A, is related to E by

$$E = P^T A.$$

In words, this says that the observed number of stock X animals (e_1) is equal to the true number in stock X times the probability that an animal from X is classified as X (p_{11}) plus the number in Y times the probability that an animal from Y is classified as X (p_{21}).

The vector A can be estimated from

$$(4)\quad \hat{A} = (P^T)^{-1}E$$

with variance estimated by the jackknife method (Hoenig and Heisey 1984) or the delta method (Pella and Robertson 1979). The approach generalizes easily to the case where animals can be classified into one of k categories (e.g. stocks). It is then necessary to invert a $k \times k$ matrix in equation (4).

This method is intuitive but no claims for statistical efficiency have been advanced for it. Furthermore, the method sometimes produces unfeasible (negative) estimates. Cook (1983) developed an intuitive method for correcting the corrected estimates, but the statistical properties induced by this modification are poorly known. Recently, Hoenig and Heisey (1987) developed the maximum likelihood (ML) estimators for the correction problem which are always feasible and are asymptotically of minimum variance, unbiased, and normally distributed. Further, they showed that when the estimates obtained by equation (4) are feasible they are also the ML estimates; Cook's method produces ML estimates only for the binomial case (two classes in the population).

Estimates of stock composition are frequently obtained by using a discriminant function to classify animals. The results are unbiased only if the assumptions are fully met. However, the results can be corrected if animals of known identity are used to develop a correction matrix. This correction procedure is nonparametric since traits are not assumed to follow any particular distribution.

Another use of the correction method might be to make estimates of age composition obtained from scales comparable with estimates obtained from spines or otoliths. Although there are a number of other potential uses (Table 2), this technique has only been used a few times in fishery work to correct estimates of stock composition (see Hoenig and Heisey (1984) and Cook (1983) for reviews).

It is important to note that the same set of correction data can be used to correct estimates from different times, locations, etc., provided only that the probabilities of misclassification (as defined by (4)) do not change. That is, the researcher's skills must not change over time and the biological characteristics used to classify the animals (e.g. color, shape) must not change between samples. The relative abundances of the traits can, and in general will, vary between samples.

TABLE 2. Applications of correction matrices in fishery surveys (from Hoenig and Heisey 1984).

Objective	Error-prone method	"Exact" method
Sex determination in fish	(1) Hematocrit[a] (2) Probe[b] (3) External characteristic[c]	(1) Otoscope (2) Surgical examination
Species identification	Morphometrics, meristics, anatomy	(1) Electrophoresis[d] (2) Latex agglutination[e]
Stock identification	(1) Morphometrics, meristics (2) Scale pattern[f] (3) Elemental composition[g]	(1) Electrophoresis (2) Sample known stocks
Age determination in pinnepeds	Tooth wear	Dentinal growth rings
Maturity stage	(1) External characteristics (2) Gross internal examination	Internal/histological examination
Composition of catch	Industry reports	Spot-checking by biologists

[a]Steucke and Atherton (1965).
[b]Glass et al. (1962).
[c]Parker (1971).
[d]Ekaratne et al. (1982).
[e]Suzuki et al. (1981).
[f]Cook (1982).
[g]Mulligan et al. (1983).

Comparative Studies

Comparative life history studies have been used to study problems in physiology, ecology, and evolution by exploring relationships in compendia of life history parameter estimates. In its simplest form, the comparative study consists of plotting one parameter against another to visually check for possible relationships. In its most sophisticated form, it can involve any of the exploratory data techniques, including classification and discrimination methods and regression and correlation analysis.

Applied ecologists have used comparative studies to seek easier ways to estimate parameters. That is, if a parameter which is difficult to estimate is functionally related to parameters which are easier to measure (or estimate), then these easily obtained parameters can be used to estimate the parameter of ultimate concern. This use of comparative studies is in contrast with studies which seek clues to basic physiological principles or taxonomic hierarchies.

One of the first comparative studies of life history parameters in fishery biology was the study of natural mortality rates by Beverton and Holt (1959) based on a compendium of mortality, growth, and longevity estimates. They showed that natural mortality is closely related to growth parameters within taxonomic orders, but failed to detect a general relationship. Taylor (1958, 1959, 1960) noted that subtle differences in temperature among stocks of a single species are correlated with growth and mortality rates. Putting these pieces together, Pauly (1980) was able to derive a multiple regression equation using data from 175 fish stocks to predict the natural mortality rate from growth parameters and mean water temperature. Using analysis of residuals, he found that only two groups, polar fishes and clupeoids, departed significantly from the relationship. Physiological considerations accounted for the departure of the polar group; a satisfactory explanation for the clupeoids is not currently available.

Another example is the prediction of the mortality rate from the maximum observed age. Ohsumi (1979) found a functional relationship between these parameters in the Cetacea. Hoenig (1983) generalized the relationship to include mollusks and fishes (Fig. 1). However, the realization that maximum observed age depends on sample size led Hoenig and Lawing (1983) to treat the maximum ages in a sample as order statistics from an exponential distribution. They thus developed an estimator based on the k oldest ages in a sample which requires a minimal amount of aging, since the oldest fishes can be found by

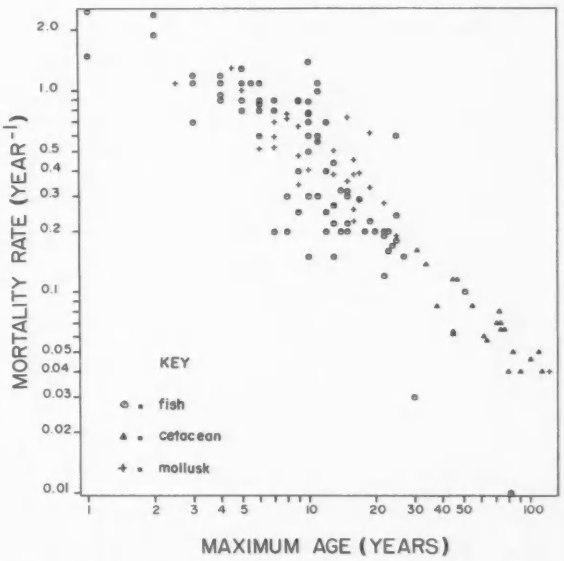

FIG. 1. Relationship between the instantaneous mortality rate and the maximum age known for 125 stocks of fish, mollusks, and cetaceans (from Hoenig 1983).

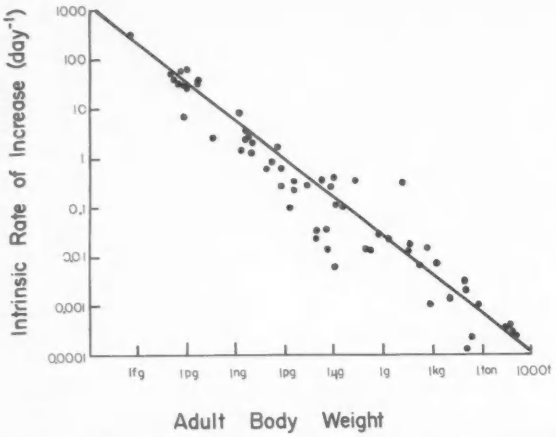

FIG. 2. Relationship between the intrinsic rate of increase of various organisms and their adult body weight (modified from Blueweiss et al. 1978 by Pauly 1982).

aging just the largest ones. Alverson and Carney (1975) developed a method for estimating the natural mortality rate from estimates of maximum age and the parameter K of the von Bertalanffy growth equation.

A well-known comparative study in fishery biology is Ryder's (1965) development of the morphoedaphic index (MEI) to estimate total potential yield from lake depth and dissolved solids. This approach has received much attention and is still the object of much interest (Jenkins 1977; Toews and Griffith 1979; Schlesinger and Regier 1983; SPOF 1982; Hanson and Leggett 1982; Oglesby et al. 1987; and references in these works). Jenkins (1977) also empirically studied the numerical relationship between predators and prey. Simple physical models for predicting potential fish yield from rivers were described by Kölbing (1978) and Welcomme (1975, 1979, 1983). Garcia and LeReste (1981) discussed use of physical variables concerning rainfall and heat flux data for short-term forecasting of shrimp yields.

A tantalizing possibility is to estimate the intrinsic rate of increase, r_m, of a population from the adult body weight. Blueweiss et al. (1978), based on work by Fenchel (1974), showed these two parameters to be highly correlated in organisms ranging in size from viruses to elephants (22 orders of magnitude). Pauly (1982) added whales and more fishes to the preceding compilation (Fig. 2) and pointed out that if further study confirms the strength of the relationship, it will be possible to employ Schaefer models without recourse to long series of catch and effort data.

Intrinsic rate of increase might be expected to be related to other life history parameters according to r–K selection theory. Heron (1972) showed that r_m is related to generation time and reproduction per generation (Fig. 3). Thus we have two independent estimates of r_m derived from life history considerations. Another compilation of life history parameters, which includes values of r_m, can be found in Caddy and Csirke (1983). One hopes that some useful generalizations will emerge as more observations are compiled and analyzed and the resulting theories are evaluated. Adams (1980) found that five other life history parameters, maximum size, growth rate, longevity, size at maturity, and natural mortality, varied in marine fishes in ways consistent with r–K selection theory. The recent volume

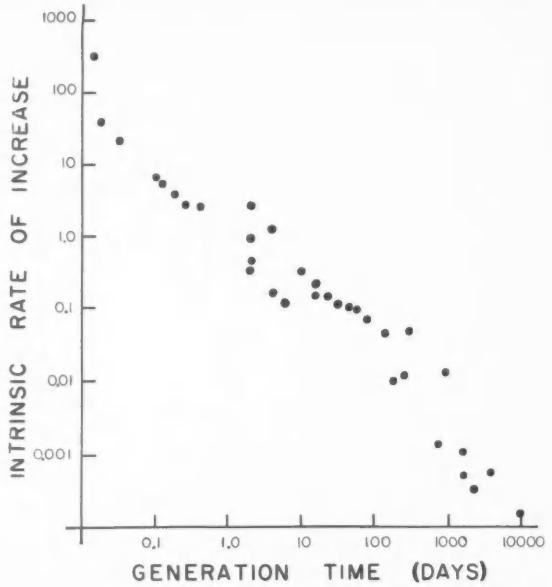

FIG. 3. Relationship between the intrinsic rate of natural increase of various organisms and the generation time (modified from Heron 1972).

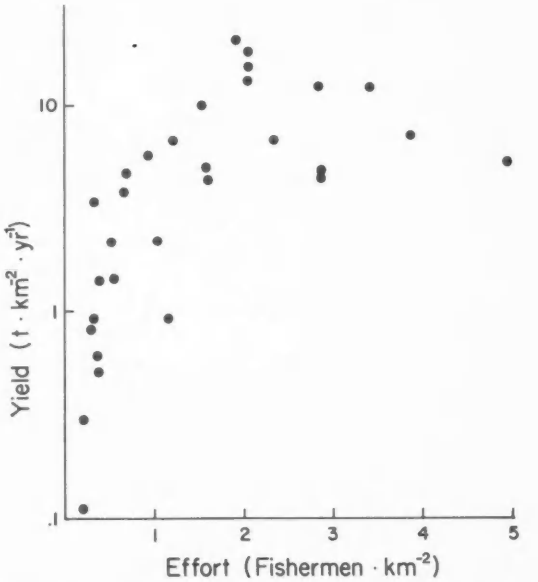

FIG. 4. Fish yields from African lakes as a function of fishing effort (from Marten and Polovina 1982).

by Calder (1984) provides a thorough examination of comparative studies and should be a useful source of ideas for further research.

A very different approach to modeling stock production without a long time series of data was developed by Munro and Thompson (1973), Munro (1980), Henderson and Welcomme (1974), Welcomme (1976), and Marten (1979). Munro showed

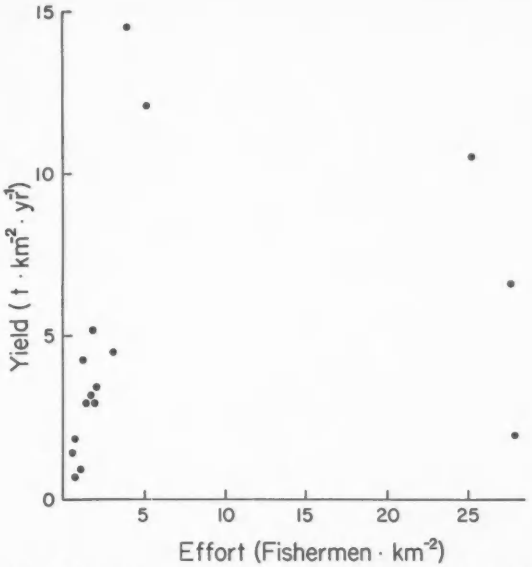

FIG. 5. Fish yields from tropical rivers as a function of fishing effort (from Marten and Polovina 1982).

that catch–effort data from ecologically similar regions in Jamaica experiencing different fishing pressures could be plotted on one graph and used to fit a production model with data from only one or two years (see Fig. 4, 5). The procedure was clarified by Caddy and Garcia (1982) and applied to a Mediterranean fishery by Garcia (1984). Goddard et al. (1987) applied the method to sport fisheries.

Csirke and Caddy (1983) presented another variation of stock production modeling in which catch per effort is plotted against total instantaneous mortality rate (Z). The method is of interest, in the context of indirect rapid assessment methodology, because the considerable problems in estimating total fishing effort are circumvented by substituting more easily obtained estimates of total mortality. Furthermore, Z can be estimated from mean length data using, for example, Beverton and Holt's (1956) equation

$$(5)\quad Z = K(L_\infty - \bar{L})/(\bar{L} - L_c)$$

where K and L_∞ are von Bertalanffy growth parameters and $\bar{L}$ is the mean length of those fish above the length L_c. If all the mortality estimates are derived from this equation, then K need not be known, since arbitrarily setting K equal to 1.0 would only serve to shift the location of the parabola along the x-axis and not change the shape. Also, L_∞ can be approximated by dividing the average length of the three largest fish known from the stock (or a similar stock) by 0.95 provided the stock is not too heavily exploited (Pauly 1984b). Another possibility is to estimate mortality from the mean weight by solving the following expression iteratively for Z (Hoenig et al. 1987):

$$(6)\quad \bar{W} = ZW_\infty \sum_{n=0}^{3} \frac{U_n(1 - (W_c/W_\infty)^{1/3})^n}{Z + nK}$$

where $\bar{W}$ is the mean weight of animals above the weight W_c, W_∞ and K are the asymptotic weight and growth coefficient, respectively, in the von Bertalanffy growth in weight curve, and $U_n = 1, -3, 3, -1$.

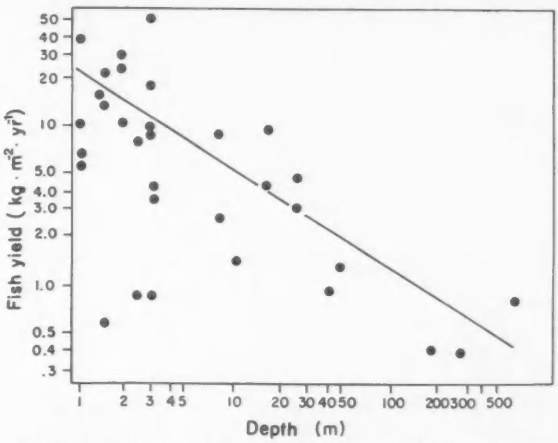

FIG. 6. Fish yields from African lakes as a function of lake depth (from Jones 1982).

Further developments are possible. For example, if only a few data points are available for a freshwater system, or if the data are too noisy for fitting a parabola, one can use an independent estimate of maximum sustainable yield (MSY) (e.g. from the MEI or other empirical relationship) as a constraint in estimating the parameters of the parabola (Hoenig and Hoenig 1986). The constraint can be introduced into the normal equations using a Lagrange multiplier. The model of interest is

$$Y_{eq} = b_1X^2 + b_2X + b_3 + \text{error}$$

where Y_{eq} is the observed equilibrium yield, the b_i are regression coefficients, and X can be either total mortality rate or fishing effort (with $b_3 = 0$ in the latter case). The predicted equilibrium yield has a maximum value of $-b_2^2/4b_1 + b_3$ which is constrained to be equal to some value "M." Then instead of

$$\text{Minimize } \Sigma(Y_{eq} - b_1X^2 - b_2X - b_3)^2,$$

the constrained least squares estimates consist of

$$\text{Minimize } [\Sigma(Y_{eq} - b_1X^2 - b_2X - b_3)^2 + \lambda(-b_2^2/4b_1 + b_3 - M)]$$

where λ is the Lagrange multiplier. The nonlinear regression routines in some of the major statistical packages allow regression with constraints.

Similarly, in Csirke and Caddy's (1983) version of the stock production model based on mortality estimates, the left x-axis intercept can be constrained to the value of an independent estimate of natural mortality rate.

Other examples of comparative studies include relating yield and community structure to physical parameters (Fig. 6–9) and relating yield to primary productivity (Fig. 10–11; also Jones and Hoyer 1982; Oglesby et al. 1987). Pauly (1984b, chap. 3) showed that comparative anatomy studies could be used to determine approximate trawl selectivity factors for soft-rayed fishes, e.g. by examining the relationship between selectivity and girth to depth ratio. A review of data compilations and comparative studies can be found in Hoenig (1982).

A conceptual framework for comparative studies was presented by Anderson et al. (1980) (Fig. 12). The different types of studies they identified can be contrasted using a simple example. Suppose one wishes to determine what factors account

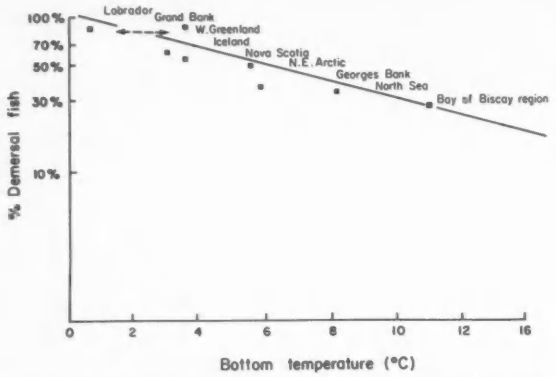

FIG. 7. Relationship between the percentage of demersal fish in the commercial landings and the bottom temperature (from Jones 1982).

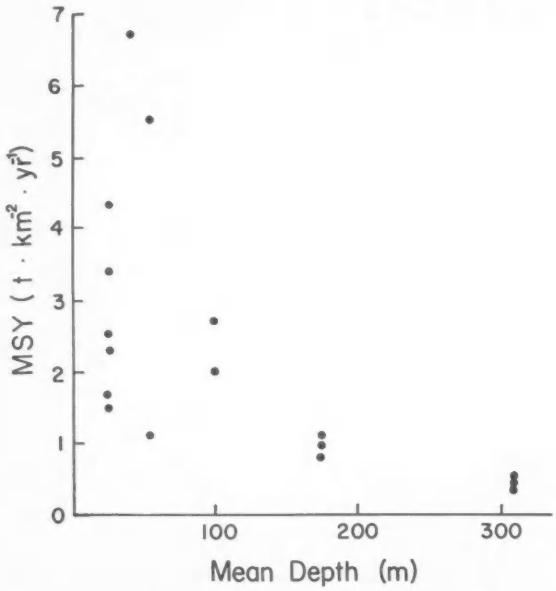

FIG. 8. Maximum sustainable yield as a function of depth for tropical continental shelf demersal fisheries ($r = -0.86$) (from Marten and Polovina 1982).

for the occurrence of undesirable events, such as winterkills or epizootics, in the lakes of a region. Suppose further that a potential "causal" factor (risk factor) has been identified such as shallow water depth. In a cohort study, a group of lakes with the factor (i.e. with shallow depth) and another group without the factor would be identified. Then the incidence of the response (winterkill or epizootic) would be contrasted in the two groups. This type of study can be conducted prospectively (identify lakes and then wait for the response) or retrospectively (identify lakes and then check the historical record to see if the response occurred). In a case control study, a group of lakes is identified in which the response is known to have occurred and, similarly, another group is identified in which the response has been absent. The occurrence of the potential causal (risk) factor is then compared in the two groups. Case control studies can only

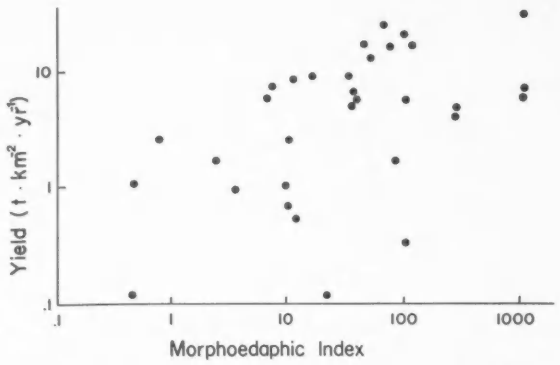

FIG. 9. Fish yields in African lakes as a function of the morphoedaphic index (from Marten and Polovina 1982).

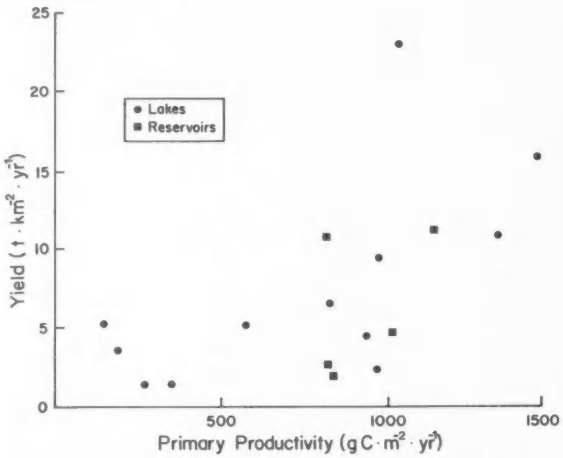

FIG. 10. Fish yields from tropical lakes and reservoirs as a function of the primary productivity (from Marten and Polovina 1982).

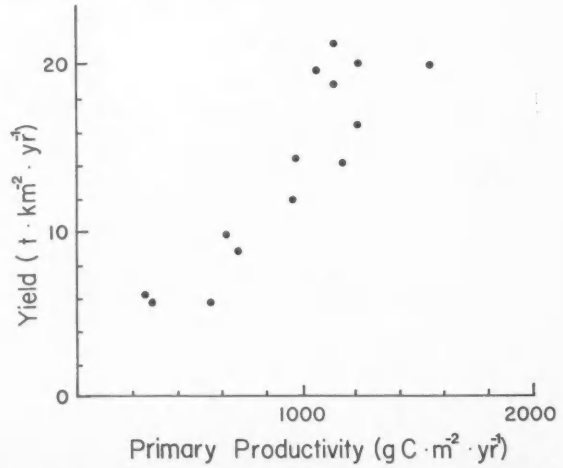

FIG. 11. Fish yields from tropical tilapia ponds as a function of the primary productivity ($r = 0.89$) (from Marten and Polovina 1982).

TABLE 3. Examples of indices in fishery science and their conversion to totals by ratio estimation.

Index	For parameter	Ratio estimator
Catch per unit effort (CPUE)	Fish population size (N)	—
Total effort (f)	Fishing mortality (F)	F = (catchability) × f
Total effort (f)	Catch (C)	C = (catch per unit effort) × f
Diesel fuel sales (S)	Effort (f)	f = (effort per liter) × S
Garbage left at boating facilities (g)	Effort (f)	f = (trips·kg garbage^{-1}) × g
Total catch (C)	Effort (f)	f = (catch per unit effort)$^{-1}$ × C
Total effort reported (rf)	Total effort (f)	f = (ratio of actual effort/reported effort) × rf
Total catch reported (rc)	Total catch (C)	C = (ratio of actual catch/reported catch) × rc
Uncalibrated measure (U)	Actual total (A)	A = (correction factor) × U where correction factor = change in A per unit of U

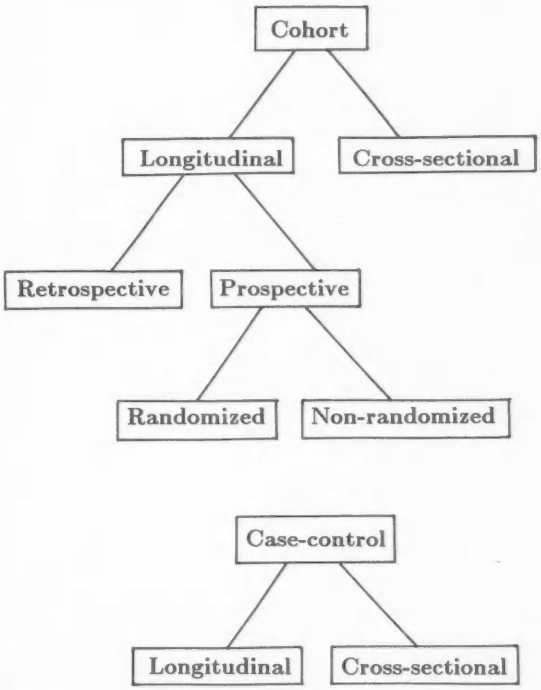

FIG. 12. A conceptual framework for comparative studies (redrawn from Anderson et al. 1980).

be conducted retrospectively. In a cross-sectional study, lakes would be simultaneously classified for the presence of the risk factor and the occurrence of the response. The type of study selected will depend on the availability of historical data and also the relative prevalences of the risk factor and the response. For example, if winterkills are uncommon, then a case control study may be preferable to guarantee adequate sample sizes in each group.

These examples demonstrate several important aspects of comparative studies: (1) comparative studies are relatively new, yet they have already produced some spectacular results; (2) vitally important parameters, which are difficult to estimate or measure directly, may be easily estimated indirectly from other parameters; (3) with time, the data bases become better, the analyses become more sophisticated, and the inferences become more insightful; (4) the empirical comparative studies can lead to better theoretical models and understanding of the systems by suggesting structural relationships which require explanation; (5) results from comparative studies can be used as preliminary estimates for traditional assessment analyses, thus providing a transition between empirical "seat of the pants" management and state of the art modeling.

A drawback of comparative studies based on literature data is that one may not have control over the quality of the data used. It may be difficult to develop objective criteria for deciding which published studies will be rejected for lack of adequate supporting information. Also, it may be difficult to obtain a complete list of pertinent studies or to obtain an unbiased sample of studies.

Holt (1962) called for more comparative studies. Recently, Banerji and Krishnan (1973) and Bakun et al. (1982) renewed the call. An international symposium held in Pallanza, Italy, in 1978 sought to review the bases for comparative studies of freshwater fisheries to promote this general approach (FAO 1980).

Indices and Ratio Estimators

Sometimes a comparative study establishes that one quantity can be used as an "index" of another quantity. For example, fishing effort is commonly used as an index of fishing mortality and catch rate as an index of population size (Table 3). The ideal index is one that is directly proportional to the quantity it replaces.

In certain situations, an index can be converted into an estimate of population total. For example, diesel fuel sales (Levi 1976) and fish landings (Ricker 1975, p. 19) are both indicators of fishing effort. The following estimators of total effort can be used:

Total effort = effort per litre × total sales
Total effort = (catch per unit effort)$^{-1}$ × total catch.

The effort per gallon and catch per unit effort ratios are determined by sampling a portion of the fleet. These procedures avoid the difficult problems of estimating relative fishing power of various types of boats and gears.

Of course, if both auxiliary variables (catch and fuel sales) are known, it is possible to use a multivariate ratio estimator for increased efficiency as follows (Sukhatme et al. 1984):

$$\text{Total effort} = wf_c + (1 - w)f_s$$

where f_c and f_s are the estimates derived from catch data and fuel sales, respectively, and w is a weighting factor for combining the estimates. If the two estimates are independent, then the optimal weight would be given by

$$w = \text{MSE}(f_s)/[\text{MSE}(f_c) + \text{MSE}(f_s)]$$

where MSE is the mean squared error. Otherwise, if catch rate and fuel consumption data are obtained from the same boats, one would need to incorporate the covariance of the auxiliary variables in the weighting calculations (Sukhatme et al. 1984).

It should be noted that only the population totals, not the individual values, are needed for the auxiliary variables when the relationship between the variables and fishing effort is linear. In the above example, if the relationship between fishing effort and fuel consumption is nonlinear, then one would have to accept added bias in the estimated total effort. However, if each individual sale of fuel is known, instead of just total sales, then a regression of effort on sales can be used to estimate the total effort for each boat. This model-building approach is discussed in more detail below under Aerial and Remote Assessments.

Williams (1978) described how auxiliary variables can be obtained almost "out of thin air." For example, to estimate the total landings in a port in a given day, one could guess at the landings for each boat and use the sum of the guesses as the population total for the auxiliary variable. Then one randomly samples some boats to estimate the ratio of actual landings to guessed landings. The observer's lack of objectivity does not cause bias in the estimate per se. However, the ratio estimation method is in general statistically biased for small samples. This bias will depend on the extent to which the relationship between guesses and actual landings violates the assumptions of the method (i.e. a linear relationship through the origin with minimal deviation from this relationship).

The variance, small sample bias, and use of the jackknife method for reducing bias is discussed for ratio estimation and related techniques in most sampling texts. Unfortunately, scant attention is usually paid to the statistical aspects of ratio estimation in fishery courses and texts despite the prevalence and importance of the method in practice.

Length as a Substitute for Age

Length frequency data contain much of the information contained in age frequency data. Thus, there has been a long history of trying to extract useful information from length frequency distributions since Petersen (1892) associated modes with age classes. Various approaches were tried over the years to improve upon Petersen's basic idea (see review by Brothers 1980), but a dependable procedure seemed elusive. Recently, Pauly developed and implemented an algorithm (in Basic) called ELEFAN I which promises to be a significant improvement (Pauly and David 1981; Pauly, 1987). The algorithm defines a set of peaks and troughs in one or more length frequency samples and then tries to maximize the goodness of fit of a growth curve by passing the curve through as many peaks and avoiding as many troughs as possible. A host of further algorithms for estimating mortality, selectivity, and population size from suitable length data have been developed for use with the original ELEFAN program. ELEFAN occupied a prominent position during the recent International Conference on the Theory and Application of Length-based Assessment (Pauly and Morgan 1987). Morgan (1987) modified the ELEFAN algorithm so that supplemental growth information, e.g. from a limited number of tag returns or age determinations, could be incorporated into the estimation procedure. Shepherd (1987a) and Pauly and Caddy (1985) described alternative algorithms to the ELEFAN method.

Estimation of mortality rates from length frequency data has proceeded along two lines. Fridriksson (1934) developed the age–length key in which an aged subsample is used to estimate the age composition in each length interval of a length frequency distribution. The method relies on the statistical concept of stratified random sampling. It qualifies as an indirect rapid assessment tool since easy to collect length data are substituted for some costly age data. Properties and modifications of the age–length key are presented in Kimura (1977), Westrheim and Ricker (1978), Clark (1981), Bartoo and Parker (1983), and Hoenig and Heisey (1987).

A classical age–length key can only be validly applied to a population with the same composition as the one from which the key was derived. Clark's method looks at the variability in length about age instead of age about length. As a consequence, his procedure can be applied to any number of populations, with varying age compositions, provided the growth rate and gear selectivity are constant. However, Clark's method assumes that the age–length key data are known without error so that the only uncertainty lies in the estimate of the length frequency of the population for which the estimate of age composition is desired. In general, age–length key data are based on small samples, since age determinations are tedious and expensive to obtain, whereas length frequency estimates are based on large samples, since measuring fish is easy. It would therefore be more reasonable to assume that most of the uncertainty lies in the age–length key part of the data. Hoenig and Heisey (1987) pointed out the similarity between the age–length key problem and the correction matrix procedure for stock composition described earlier. Their ML estimation procedure allows for stochastic error in both the length frequency sample and the age–length key data with the amounts of error depending on the sample sizes.

Beverton and Holt (1956, 1957, p. 22) pioneered the other approach of estimating the total mortality rate directly from length statistics when growth rates are known (see equations (5) and (6)). A number of extensions have been developed over the years which are reviewed by Hoenig et al. (1983) and Pauly and Morgan (1987).

A problem with using simple statistics such as mean or median length to estimate the total mortality rate is that one cannot judge the validity of the basic assumptions. As Powell (1979) has shown, even a cursory examination of a length frequency distribution can give useful insights into the population dynamics of a stock (Fig. 13). Thus, it is significant that Jones (1981) developed a regression technique for length frequency data which allows one to visually inspect the goodness of fit. Jones' technique consists of plotting the cumulative catch above a length L against $\log_e (L_\infty - L)$. The resulting slope (except at the ends of the line segment) estimates Z/K. If L_∞ is not known, it can be estimated by iteratively seeking the value of L_∞ which maximizes the coefficient of determination. Pauly

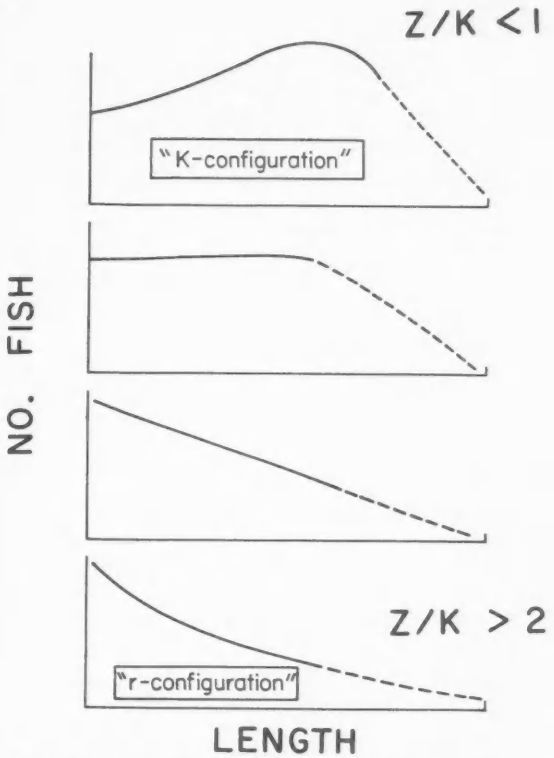

FIG. 13. Relationship between the ratio of Z/K (mortality to growth coefficient) and the shape of a length frequency distribution (from Pauly 1982).

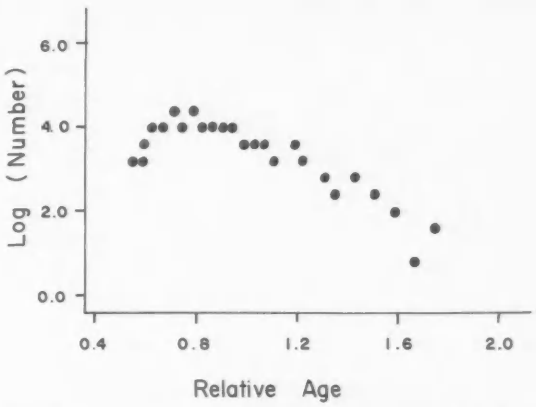

FIG. 14. A length-converted catch curve for Lake Minnetonka, Minnesota, largemouth bass (*Micropterus salmoides*). Ordinate is the logarithm of the number of fish in a length interval; abscissa is the relative age at the midpoint of the length interval defined as $t' = -\log_e(1 - L/L_\infty)$ where L_∞ is the asymptotic size. The slope of a regression line fitted to the descending right limb estimates $1 - Z/K$. (Data courtesy of M. Ebbers, Minnesota Department of Natural Resources.)

(1983, 1984a, 1984b) advocated the slightly different approach of analyzing a catch curve based on relative ages derived from a length frequency sample (Fig. 14). Since Jones' method uses cumulative catch, which is a monotonic function of $\log_e(L_\infty - L)$, the slope will always be significant. Thus, Pauly's method seems to be on sounder statistical footing, but further work is necessary to study the properties of these techniques.

It is now feasible to think in terms of length-based virtual population analysis (VPA). The approach has been pioneered in papers by Jones (1974, 1979, 1981, 1984) and Pauly (1984b). Pope and Jiming (1987) developed a length-based multispecies cohort analysis. Holt (1977) proceeded in a different direction and considered the estimation of population size of sperm whales from changes in the mean size in the catches.

It is clear that there is now considerable interest in the development of length-based assessment techniques. The estimation of growth parameters from length data is mainly of interest in tropical regions and for use on crustaceans, since direct age determinations are difficult in these situations. Short-term forecasting (Shepherd 1987b), mortality estimation, and estimation of population size are almost universally of interest.

Assessment by Analogy

Intuitive judgments about the fisheries in a lake can be sharpened by defining empirical indices that can be used for comparing ecologically similar lakes. The basic idea is that if easily measured statistics for a given lake, such as test netting data, are similar to lakes known to be in acceptable condition, then the lake is probably also in good condition. Mean length might be plotted against standard deviation to develop empirical probability densities as a basis for comparison, and to try to cluster similar lake communities. Predatory–prey ratios and other indicators of community structure could be tabulated. These statistics can be used to "flag" lakes potentially in need of further study.

As an example, mean lengths and standard deviations of bluegill (*Lepomis macrochirus*) and northern pike (*Esox lucius*) were obtained from routine survey files for 41 lakes in central Minnesota with permanent fish populations (Fig. 15). Mean length appeared to be unrelated to standard deviation among pike populations ($r^2 = 0.015$, $p = 0.550$). Hence, unusual occurrences were taken to be indicated by extreme values of either variable. Among bluegill populations, mean length appeared to be negatively correlated with standard deviation ($r^2 = 0.161$, $p = 0.002$). Unusual populations were considered indicated by extreme outlier scores (Cook 1977) of data points about a linear regression line (e.g. those points with p values less than 0.10). This procedure is intended as an exploratory tool, not as a formal test of hypothesis, and is at any rate tentative.

An alternative approach was developed by Tonn et al. (1983) who used various multivariate statistical techniques to classify lakes and relate community structure to habitat variables. They used these results as a basis for developing management strategies.

Ryder and Edwards (1985) recommended a holistic approach to ecosystem quality and suggested that key indicator species be monitored as guides to the rest of the system. The evaluation of impacts on key species, known as Representative Important Species (RIS), is a standard approach to meeting the assessment provisions of sections 316a and 316b of the *United States Federal Water Pollution Control Act of 1972* (see EPA 1977a, 1977b). Regardless of what one thinks of this strategy, it is likely to play a prominent role in ecological impact assessment for many years for want of a better approach. It is also clear that

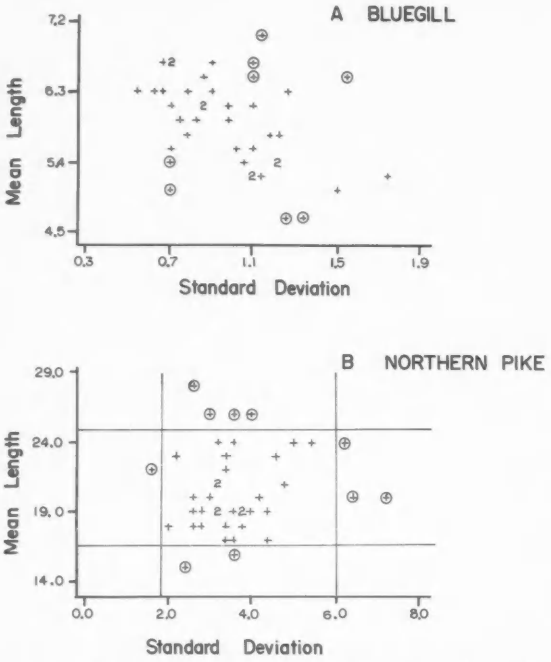

FIG. 15. Plot of mean length versus standard deviation for 41 populations of (A) bluegill and (B) northern pike. Lines and circles indicate "unusual" conditions (see text).

"key indicator" lakes and streams will be used to monitor regional problems such as acid precipitation. There is a trade-off between studying more lakes and studying lakes in more detail. The importance of this trade-off diminishes when quicker study techniques become available. It is hoped that a spectrum of approaches with varying data requirements can be developed to suit individual needs based on cost, data availability, and political considerations.

Volunteered Data

Fishermen can be enlisted to provide a variety of types of information. The trick is to estimate the reliability of the data and to deal with systematic errors.

One of the earliest uses of volunteer sportsmen was in the analysis of banding and tagging data. A highly sophisticated set of models and procedures, developed largely for bird banding studies, are now available to fishery biologists (Otis et al. 1978; White et al. 1982; White 1983; Brownie et al. 1985). Unknown and changing reporting rates are handled by marking animals at two or more times. Then, differences in return rates for the cohorts in a given year can reasonably be attributed to mortality (provided tag shedding and other factors can be accounted for).

Under suitable supervision, fishermen can provide quality information on catch rates, fish size frequencies, geographic distribution, etc., as well as quantitative tag return rates and biological samples. Ebbers (1987) enlisted anglers to keep detailed diaries and also collected data at sport fishing tournaments. The data collected from both sources were comparable with data collected on biological surveys but entailed less manpower on the biologists' part.

In Yellowstone Park, fishermen are asked to voluntarily submit reports on their fishing trips. A creel clerk makes spot checks so that inverse regression (calibration) can be used to adjust the estimates for reporting bias (R. Gresswell, pers. comm.). Further consideration of creel survey methods is given in the next section.

Aerial and Remote Assessments

The use of aircraft and remote sensing satellites may seem inconsistent with the rapid assessment goal of stretching the research budget. However, in many cases, assessments from the air can be highly cost effective. Some useful remote sensing data, generated as a by-product of other projects, can be obtained for a nominal charge. (Use of inexpensive kites has also been tried (Scoffin 1982).)

Aircraft can cover in a few hours what a team of biologists on the water might take several days to visit. Aerial observers can count fishing vessels by size and gear (and other boat types), count fixed location gear, count and estimate the size of fish schools and identify them to varying degrees, count salmonid nests (redds) in streams, map reefs and marshes, etc. (Squire 1983; Parrack 1976; Heggberget et al. 1986). Biotic and abiotic environmental conditions such as chlorophyll, phytoplankton taxa, riparian vegetation, surface temperature, wave height, and current characteristics can be quantified (Klemas et al. 1980; Brahma et al. 1983; Crouse and Findley 1984; Feldman et al. 1984; Fu and Chelton 1984). In addition, the observers can provide public services such as relaying the locations of fish schools and basking tunas and billfish, reporting mariners in distress, hazardous obstructions, etc.

These methods enter the realm of indirect rapid assessment methodology when there is visibility bias which must be corrected (e.g. Cook and Jacobson 1979), when raw counts from the air must be apportioned to various categories based on surface studies of relative abundances (ratio estimation), or when remote sensing signals need calibration.

When the study area is too large to be completely observed, one can use line transect methods to count boats and fixed gear (see Burnham et al. (1980) for a review). Statistical and practical aspects of aerial sampling are discussed by Jolly (1979) and Jolly and Watson (1979).

An alternative is to make two (or more) independent counts in which each object is uniquely identified (e.g. by noting its location on a map or recording its license number). The results can then be analyzed using mark–recapture methods. That is, one survey "marks" the boats by uniquely identifying them; the other survey "recaptures" a boat when a previously identified boat is spotted (Magnusson et al. 1978). If the whole area is not censused, then the boats must mix randomly between observation periods or the observation trips must follow random paths. Mark–recapture methods have been tried (without the use of airplanes) on Liverpool taxicabs (Bishop and Bradley 1972) and creeled fish (Regier 1971).

Another strategy that can be applied to catch and effort surveys is to correlate observations at one time (of day, of the week) with the total over a longer interval. For example, Parker (1956) found that sport fishing effort at noon was highly correlated with the total daily fishing effort. This aspect has also been investigated by Powell and Bowden (1981). This suggests the use of a model-based approach to sampling whereby observed count or effort data can be fitted to a model by regression techniques. Total effort can then be estimated by integrating the

regression equation over the appropriate time interval (e.g. season). Variance, bias, and design considerations were discussed by Hoenig et al. (1986).

Hydroacoustic surveys and use of resistivity fish counters in streams (Dunkley and Shearer 1982) are conceptually similar to aerial surveys in that the recorded signals must be calibrated with biomass or numbers and apportioned to species or size groups. The use of automatic traffic counters at fishing access points also generates data which need calibration.

Perspective

Does the foregoing constitute the basis of a general strategy for managing aquatic resources? Or have we simply presented a collection of more or less unrelated techniques?

Implicit behind the use of all of these techniques is the idea that a biologist, faced with a choice of methods, may choose a less accurate method if the savings over using a more accurate method are substantial. The lower cost may allow one to process a large enough sample so that better results can be obtained over the use of a more accurate/precise (and more expensive) technique applied to a smaller sample. But even if the less expensive technique necessarily gives inferior estimates, its use may still be warranted so that a greater number of samples (of species, geographical areas, etc.) can be processed. Greater detail in the assessment of a fishery may be preferable to greater accuracy for a segment and no information for the rest of the fishery. This may be particularly important to consider in multispecies stock assessments.

Of course, indirect rapid assessment methods do not have to be crude. In many instances, "quick and dirty" techniques have evolved into "quick and sophisticated" procedures. The use of length-based assessment and hydroacoustics has already been mentioned. Even "rules of thumb" can be improved or expanded. For instance, Beddington and Cooke (1983) evaluated Gulland's suggestion that MSY may be approximated by $0.5MB_0$ (where M is the instantaneous natural mortality rate and B_0 is the virgin biomass). They proposed simple modifications to protect against recruitment problems.

It is reasonable to expect that ecological theory will benefit from the routine use of rapid assessment methodology for fisheries management. The benefits will accrue from the compilation of comparative data, the search for functional relationships, and the increasingly detailed studies possible with some rapid methods.

It is difficult to combine these ideas into a definition of indirect rapid assessment methodology. But one cannot propose a concept without attempting to define it. Perhaps the following will serve as a working definition:

> Rapid assessment methodology aims to increase the amount of assessment work that can be accomplished under fixed manpower and budget constraints by seeking faster and less expensive methods. Indirect rapid assessment methodology seeks to exploit the functional relationship between easily measured or estimated quantitites and the parameters of ultimate concern. Indirect methods may sometimes be chosen for their ability to provide greater detail in assessments (even though this may sometimes be at the expense of less accuracy or precision).

The rapid assessment approach is almost universally applicable. In tropical waters, a single trawl haul may contain more than 100 species for which basic life history parameters are largely unknown. This led Pauly (1980, 1982, 1984b) to advocate a set of rapid assessment techniques for tropical fish stocks. His procedures should also find use in other regions. In the major groundish fisheries of the North Atlantic, basic parameters have long been known for the most important species, yet stock identification is still a large problem, and attempts to develop working multispecies models are hindered by lack of information on the minor species. In the State of Minnesota, there are some 10 000 lakes; hence, it is not an exaggeration to say that there are more than 10 000 stocks to manage. Most of the managers of these fisheries would probably agree that some information is better than no information. Presumably, rapid assessment techniques could go a long way in filling their needs.

In the universities, students are taught to use state-of-the-art technology and are counseled to learn statistics in order to increase the quality and quantity of assessments. Perhaps it is time to counsel them to also look to where the "quick and dirty" approach can lead. We may develop a well-stocked toolbox of rapid assessment techniques ranging from crude to highly sophisticated. Perhaps the dictum "correlate, calibrate, and compare" is worth remembering.

Acknowledgments

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Optimal $F_{0.1}$ Criteria and Their Relationship to Maximum Sustainable Yield

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There is a unique size of entry into the fishable population that maximizes yield per recruit when an $F_{0.1}$ fishing criterion is applied to the simple theory of fishing developed by Beverton and Holt in 1957. I define such a pair of parameters (size of entry, $F_{0.1}$ value) to be the optimal $F_{0.1}$ criteria and show that they are characterized by the single quantity M/K. A quantitative relationship is established between maximum sustainable yield and the optimal $F_{0.1}$ criteria for a model population where recruitment is governed by a Ricker stock–recruitment function. This new theory is applied to three fish stocks: Pacific halibut (*Hippoglossus stenolepis*), western Lake Erie walleye (*Stizostedion vitreum vitreum*), and Bering Sea Pacific cod (*Gadus macrocephalus*).

Il n'existe qu'une taille d'entrée dans la population exploitable qui permet de maximiser le rendement par recrue lorsqu'un critère de pêche au niveau $F_{0.1}$ est appliqué conformément à la théorie simple de pêche élaborée en 1957 par Beverton et Holt. L'auteur définit un couple de paramètres de ce type (taille de recrutement, valeur au niveau $F_{0.1}$) comme critères optimaux au niveau $F_{0.1}$ et montre qu'ils sont caractérisés par la quantité unique M/K. Une relation quantitative est établie entre le rendement maximal soutenu et les critères optimaux au niveau $F_{0.1}$ pour une population modèle dont le recrutement est régi par une fonction stock–recrutement de Ricker. L'auteur applique cette nouvelle théorie à trois stocks de poissons : ceux du flétan du Pacifique (*Hippoglossus stenolepis*), de la morue du Pacifique (*Gadus macrocephalus*) de la mer de Bering et du doré jaune (*Stizostedion vitreum vitreum*) de la partie ouest du lac Erié.

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Yield theory for fish populations can, for the most part, be classified into two distinct categories. First, there are the theoretical results based on mathematical biological models. Second, there are the empirical relationships developed between potential yield and certain characteristics of the ecosystem under study (such as morphoedophic indices, Ryder et al. 1974). In this paper, I discuss only single-species biological models and present new results on yield per recruit theory for age-structured populations.

Age-structured (so-called dynamic pool) models explicitly represent a population as a group of cohorts that both grow and suffer mortality as time passes. Recruitment of a new cohort to the fishable age-classes is assumed to be either dependent in some way on parent stock size or else independent of parent stock over the range of stock sizes used in the analysis. That latter assumption about recruitment leads to a consideration of the classical yield per recruit problem where we seek to fish a given cohort in such a way that its full growth potential is realized (subject to certain constraints on the age selectivity of fishing).

Yield per recruit analysis has been an important basis for scientific advice on size limits and fishing effort regulation for decades. Its popularity is largely related to the observation that data on recruitment indicate substantial year-class fluctuations for many fish stocks which appear unrelated to parent stock size estimates. When recruit abundance is independent of parent stock size, then all that fisheries management can do is to take advantage of whatever recruitment is available according to a yield per recruit analysis. Estimation of appropriate F, fishing mortality rate (see glossary of key parameters), and/or size of recruitment to the fishery is greatly facilitated by the so-called simple theory of fishing developed by Beverton and Holt (1957), who gave explicit formulae for the yield available from a given cohort over its fishable life span as a function of mortality, growth, and size of recruitment into the fishery. The fishing mortality rate that maximizes yield per recruit for a given age of entry is defined as F_{max}.

In recent years, the futility of using F_{max} as a management level has been reinforced (Anthony 1982). There are various reasons why F_{max} may be undesirable. Usually the yield per recruit curve is nearly flat in the neighborhood of the maximum, and thus, moving from a fishing mortality rate that takes 99% of the yield available at F_{max} to a fishing mortality rate equal to F_{max} will require a disproportionate increase in fishing effort (Gulland 1968) and hence is economically inefficient. In addition, when there is a relationship between recruitment and fishable stock abundance, then F_{max}, which is based solely on yield per recruit analysis, is larger than the fishing mortality rate that produces maximum sustainable yield, unless strong density dependence is present in the recruit relationship (Deriso 1982).

One alternative to F_{max} that has had recent wide application in fisheries management has been to target fishing mortality rate at

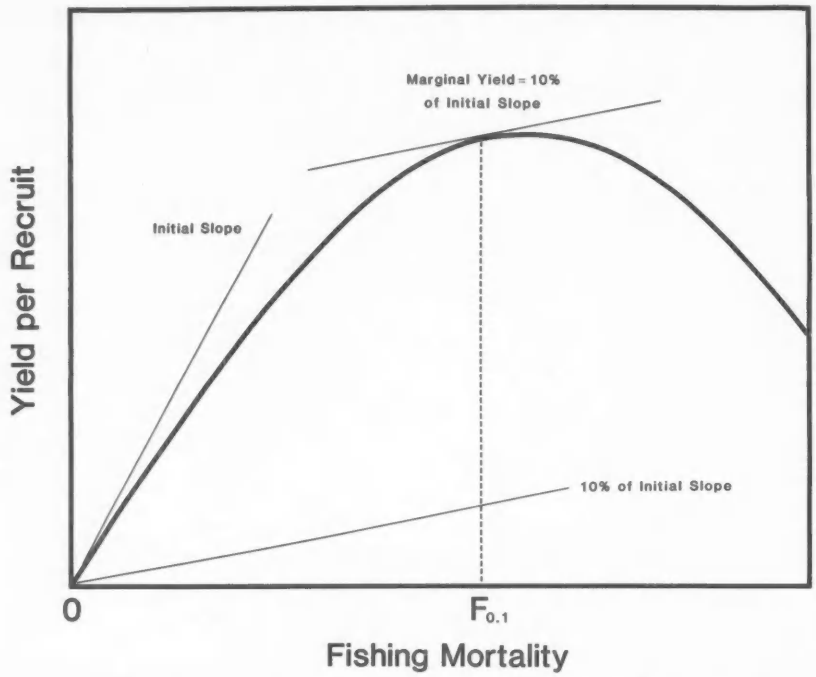

FIG. 1. Determination of $F_{0.1}$ fishing mortality, adapted with modification from Gulland and Boerema (1973).

$F_{0.1}$, which is essentially the level of F for which the marginal increase in yield per recruit due to a small increase in F is 10% of the marginal yield per recruit in a lightly exploited fishery (Fig. 1). Assessments for $F_{0.1}$ have been a regular feature of assessments by ICES working groups in recent years (R. J. H. Beverton, pers. comm.). From Doubleday et al. (1984) we read, "Most of the fish stocks within the Canadian Atlantic zone are currently managed at the level of fishing corresponding to $F_{0.1}$ ... ."

The $F_{0.1}$ criterion is not uniquely defined for a given fish stock unless age of recruitment into the fishery, or more generally, age selectivity of fishing mortality, is fixed at some predetermined amount. For the simple yield per recruit theory in Beverton and Holt (1957), however, there is a unique size of entry into the fishable population that maximizes yield under a $F_{0.1}$ fishing criterion. I define this as the optimal $F_{0.1}$ criteria, which consists of an optimal size (or age) of entry and corresponding $F_{0.1}$ fishing mortality rate. I show that optimal $F_{0.1}$ criteria can be characterized by the single quantity M/K (ratio of natural mortality rate M to the von Bertalanffy growth parameter K) and present several results which allow the reader to apply these results to their particular fish stock of interest. The origin of the quantity M/K is Beverton and Holt (1959).

One limitation of yield per recruit theory is that it does not take account of stock–recruitment relationships. Results are presented on the relationship between optimal $F_{0.1}$ criteria and exploitation rates that maximize yield when a Ricker (1954) stock–recruitment relationship is present. And more generally, I show that the consequence of fishing at $F_{0.1}$ can be characterized by a function of the Ricker stock–recruitment parameter α.

As will be shown in what follows, the ratio M/K uniquely characterizes the optimal $F_{0.1}$ criteria and thus takes on a special importance in assessment. In this paper, techniques for estimating this ratio are discussed that allow us to approximate the optimal $F_{0.1}$ criteria for even poorly documented fish stocks. Thus, a feasible and sensible scheme of rapid stock assessment and management is possible. Finally, I illustrate application of the optimal $F_{0.1}$ criteria to three fish stocks: Pacific halibut (*Hippoglossus stenolepis*), western Lake Erie walleye (*Stizostedion vitreum vitreum*), and Bering Sea Pacific cod (*Gadus macrocephalus*).

Basic Yield per Recruit Theory

Analysis of yield available from a given cohort is the principle topic of yield per recruit theory. The simple yield theory developed by Beverton and Holt (1957) gives total yield available from a cohort when (1) the rates of fishing mortality and natural mortality are constants independent of age (above some age, t_c, of recruitment into the fishery) and (2) growth is given by the von Bertalanffy growth curve. A convenient parameterization, in dimensionless terms, of yield per recruit is given in Beverton (1963), namely:

$$(1)\quad Y' = Y/(RW_\infty) = E \sum_{n=0}^{3} \frac{U_n(1-c)^n}{1+n(1-E)/m}$$

where $U_n = +1, -3, +3$, and -1 for $n = 0, 1, 2$, and 3, respectively, $E = F/(F+M)$ = rate of exploitation, $c = L_c/L_\infty$ = length at recruitment divided by maximum length, $m = M/K$ = natural mortality rate M divided by growth parameter K of the

von Bertalanffy length equation, R = abundance of the year-class when they reach recruitment length L_c, Y = yield, and W_∞ = asymptotic weight parameter, which is proportional to the asymptotic length, L_∞, of the von Bertalanffy equation raised to the third power. Y' is therefore the life-time yield from a year-class recruited at length L_c, expressed as a fraction of the maximum possible weight (RW_∞), if all recruits survived to reach weight W_∞. We also would like to examine the effect of changing L_c on yield available from a cohort, so we reparameterize equation (1) following Beverton and Holt (1964) as

$$(2) \quad y = Y/N(t_0)W_\infty = (1 - c)^m Y'$$

where $N(t_0)$ is abundance of a year-class at the hypothetical age t_0 and t_0 is the age parameter of the von Bertalanffy equation. Note that $R = N(t_0) \exp(M(t_0 - t_c))$ for age of recruitment (t_c).

Relative yield (y) is the same as Y' except that R is replaced by cohort abundance at the arbitrary age t_0. Notice that y is a function of three parameters (E, c, and m). Two of these parameters (E and c) are control variables available for manipulation by fisheries management, while (m) is the only biological parameter needed for a yield per recruit analysis. Relative yield available for a given value of the biological parameter m can be completely described in a yield isopleth diagram. The diagram can be constructed with exploitation rate E on one axis, relative size c on the perpendicular axis, and contours in the diagram that connect equal values of relative yield. Originally developed by Beverton and Holt (1957, e.g. p. 326), yield isopleth diagrams show the trade-offs required between recruitment size and fishing mortality to produce given levels of relative yield. Yield isopleth values can be found in tabular form for equation (1) and certain values of m in Beverton and Holt (1964) and Gulland (1969). The maximum possible value of y (= y^*) is that corresponding to an infinitely large F applied to a cohort when it reaches a size c (=c^*) where the biomass of the year-class reaches its maximum value. The maximum possible yield is a convenient benchmark for comparison with the optimal $F_{0.1}$ criteria described later. In general, the maximum possible yield for a given year-class occurs at age t^* where

$$\left.\frac{d(N(t)w(t))}{dt}\right|_{t=t^*} = 0.$$

Here, $N(t)$ is abundance of a year-class in the absence of fishing and $w(t)$ is per capita weight at age t. For a constant natural mortality rate (M) and the von Bertalanffy growth equation, the age at which a year-class reaches its maximium biomass is given in Alverson and Carney (1975) as

$$t^* = t_0 + \frac{1}{K} \ln(3K/M + 1),$$

or in terms of relative quantities c and m, we have

$$(3) \quad c^* = \frac{1}{1 + m/3},$$

and the corresponding maximum possible yield (y^*) is given as

$$(4) \quad y^* = (c^*)^3(1 - c^*)^m.$$

The maximum yield obtainable from a year-class is given by equation (4) and occurs by completely and instantaneously fishing out that year-class when it reaches the size given by equation (3). For stocking programs, such as lake trout (*Salvelinus namaycush*) in Lake Michigan, equation (4) may be an appropriate goal if maximum yield is the main management objective. In reality, it may be physically and economically impossible to generate a fishing effort large enough to completely fish out a year-class; thus, yields may only approach the level derived in equation (4). These results have been extended to an economic setting in Clark (1976), who also provided theory for determining minimum (and maximum) size limits when fishing mortality is constrained to lie below a maximium level.

The $F_{0.1}$ Criterion

The level of fishing mortality at $F_{0.1}$ is defined formally for a given recruitment age as that level of F where

$$(5) \quad \left.\frac{\partial Y'}{\partial F}\right|_{F=F_{0.1}} = \frac{(0.1)\partial Y'}{\partial F}\bigg|_{F=0},$$

or by reparameterizing in terms of the exploitation rate $E = F/(F + M)$, an equivalent $E_{0.1}$ level is given by

$$\left.\frac{\partial Y'}{\partial E}\right|_{E=E_{0.1}} = \frac{0.1}{(1 - E_{0.1})^2}\left.\frac{\partial Y'}{\partial E}\right|_{E=0},$$

which also holds true for differentiation of relative yield (y) in equation (2).

The $F_{0.1}$ level for any given weight at age function $w(t)$ and knife-edge recruitment at age t_c can be characterized by expanding equation (5) to get

$$\int_{t_c}^{\infty} e^{-Z(x-t_c)}w(x)dx - F_{0.1}\int_{t_c}^{\infty}(x - t_c)e^{-Z(x-t_c)}w(x)dx = 0.1\int_{t_c}^{\infty} e^{-M(x-t_c)}w(x)dx$$

and solving for $F_{0.1}$ to get

$$(6) \quad F_{0.1} = \frac{1 - 0.1\,\mathrm{BPR}(F = 0)/\mathrm{BPR}(F = F_{0.1})}{t_w - t_c}$$

where BPR(F = –) is the total biomass generated by a recruit of age t_c over its entire lifetime when fishing mortality is held at F = – and where t_w is the average age of a unit of biomass for a cohort during its fishable lifetime. That is to say,

$$t_w = \frac{\int_{t_c}^{\infty} xB(x)dx}{\int_{t_c}^{\infty} B(x)dx}.$$

where $B(x)$ is biomass per recruit of the exploited cohort at age x. An upper bound can be developed for $F_{0.1}$, since the cumulative biomass per recruit BPR is larger when $F = 0$ than when $F = F_{0.1}$. Putting that inequality into equation (6), we see that

$$F_{0.1} < \frac{0.9}{t_w - t_c}.$$

The $F_{0.1}$ criterion is not uniquely defined for most fish stocks unless age of recruitment, or more generally, age selectivity of fishing mortality, is fixed at some predetermined amount. In Fig. 2, relative yield y for the $F_{0.1}$ policy and $E_{0.1}$ are graphed as a function of relative recruitment length c for two values of the biological parameter m. As seen in this figure, relative yield peaks in each of these curves. Indeed, by insisting that we fish at

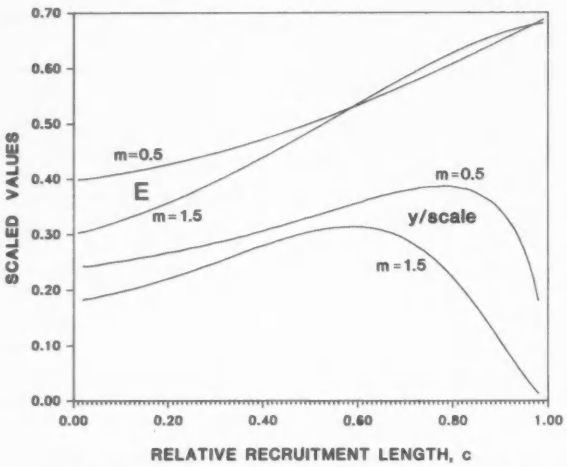

FIG. 2. Relative yield y and exploitation rate E from the $F_{0.1}$ criteria as a function of relative recruitment length c and two values of m (0.5, 1.5). Relative yields (y) have been rescaled, scale = 0.15 for $m = 1.5$ and scale = 0.5 for $m = 0.5$.

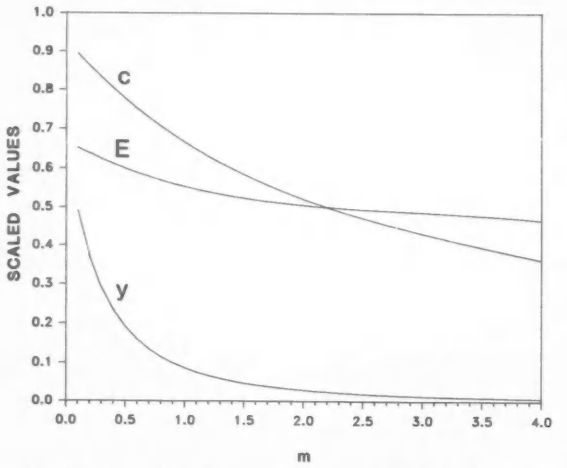

FIG. 3. Relative yield y, relative size of entry c, and exploitation rate E for the optimal $F_{0.1}$ criteria are given as a function of $m = M/K$.

$F_{0.1}$, there is an optimal age of entry, or relative size, c_{opt}, which maximizes yield per recruit, and in equation (2) this optimal $F_{0.1}$ criterion depends solely on the biological parameter m. We no longer have independent controls, E and c, since $E_{0.1}$ is now a function of c.

Optimal $F_{0.1}$ Criteria

A complete description of the optimal $E_{0.1}$ criteria was calculated for the simple yield theory of equation (2). These results are presented in Fig. 3, 4, and 5. In Fig. 3, optimal c values and the corresponding $E_{0.1}$ and relative yield y are given for values of m ($=M/K$) ranging from 0.1 to 4.0. We see that the $E_{0.1}$ values are fairly constant over a range of m values (1.0–4.0) but change rapidly for low values of m. In order to compare the optimal $E_{0.1}$ criteria with the absolute maximum yield possible, as formulated in equation (4), Fig. 4 was constructed. Over the range ($1 < m < 4$), relative yield with optimal $F_{0.1}$ criteria is 82–83% of the maximum possible, and the size of recruitment c_{opt} is 83–90% of the size c^* where natural biomass of a cohort peaks. Also shown in Fig. 4 is ratio of $F_{0.1}$ to M. Over the range ($1 < m < 4$), optimal $F_{0.1}$ criteria have $F \approx M$ (actually, F/M ranges from 0.88 to 1.25 here). Thus, this analysis provides theoretical conditions for the commonly used scientific advice to set $F \approx M$ (Gulland 1970) when dealing with a poorly understood fish stock. More importantly, these results provide a guide to appropriate F/M ratios and minimum size limits, since ratios of M/K should be available (or easily approximated) even for poorly understood stocks (e.g. Pauly, 1980).

One issue left from the analysis to this point is the effect that fishing has on future recruitment when a stock–recruitment relationship is present. Especially important is whether or not $F_{0.1}$ criteria place unrealistic demands on the reproductive capability of the adult stock. A quantity to measure those demands is the production of recruit biomass per unit adult biomass in the stock (i.e. $B(t_c)$/total adult biomass), which is defined here as the recruit production fraction. I work with production in units of biomass for two reasons: (1) yield taken in most fisheries is managed in units of biomass and (2) yield per recruit formulae are in units of biomass. On a stock–recruitment graph, the slope of the recruit biomass curve at the origin is the theoretical maximum recruit production fraction for the stock. With a series of historical data, average annual recruit production can be estimated. Those estimates can then be compared with scaled recruit production fractions (rpb), which are calculated as

$$\text{rpb} = B(t_c)/(MB)$$

where

$$B = \int_{t_c}^{\infty} B(x)dx$$

is approximately the average biomass of the fishable stock at equilibrium.

Figure 5 shows the scaled production fractions for the $F_{0.1}$ criteria of equation (2). The scaled production fractions decline gradually for $1 < m < 4$, ranging from around 1.0 to 1.5. For a given fish population, we can take its (m) estimate, read off the corresponding scaled production fraction (rpb) from Fig. 5, and then compare it with measured values of production for that stock to see if the optimal $F_{0.1}$ criteria places reasonable demands on the stocks' reproductive capacity. Such a comparison is made in Anonymous (1984a); recruit production fractions were calculated for all values of F in a yield per recruit analysis of four fish populations of the North Sea and then compared with data on actual recruitment and stock size. I should mention here one shortcoming of the numbers in Fig. 5 is that they use adult biomass (all fish above recruitment size c_{opt}) as the measure of parent stock.

A more interesting and difficult issue is the relationship between optimal $F_{0.1}$ criteria and exploitation rates that maximize yield when a stock–recruitment relationship is present. Let us denote a fishing mortality rate that maximizes yield, when a stock–recruitment relationship is present, as F_{msy}. At equilibrium, maximum sustainable yield (MSY) is harvested when $F = F_{msy}$. I have analyzed the situation where the $F_{0.1}$ criteria are based on the simple yield per recruit theory of equation (2) and where recruitment *biomass* is determined by a Ricker stock–

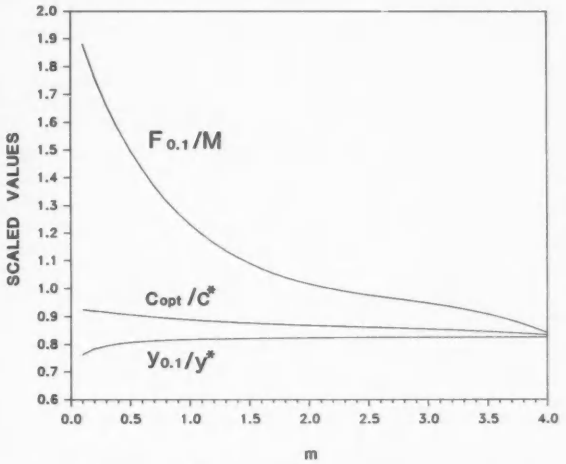

FIG. 4. Ratios of fishing mortality to natural mortality F/M, ratio of relative entry size to size where natural biomass peaks c_{opt}/c, ratio and of relative yield to maximum possible yield y/y^* for the optimal $F_{0.1}$ criteria are given as a function of $m = M/K$.

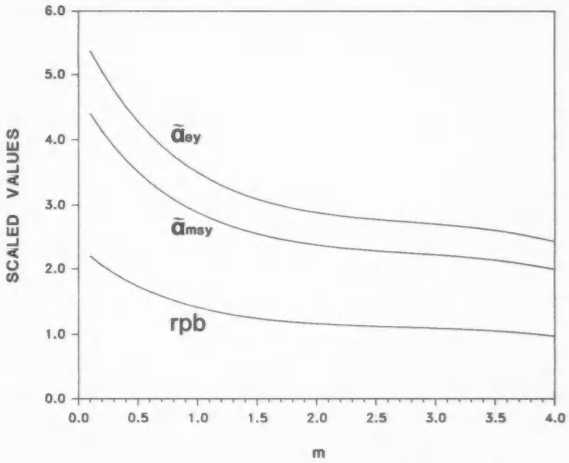

FIG. 5. Stock–recruitment characteristics for the optimal $F_{0.1}$ criteria are given as a function of m. Shown are the scaled recruit production fraction rpb, the scaled slope parameter of a Ricker stock–recruitment model $\tilde{\alpha}_{msy}$ where $F_{msy} = F_{0.1}$, and the scaled slope parameter $\tilde{\alpha}_{ey}$ where $F_{ey} = F_{0.1}$.

recruitment curve:

$$B(t_c) = \alpha B \exp(-\beta S).$$

In Appendix A, I show that $F_{0.1}$, which is based solely on yield per recruit analysis, equals F_{msy} when a scaled parameter in the Ricker curve, $\tilde{\alpha} = \alpha/M$, satisfies the equality

$$(7)\quad \tilde{\alpha} = \frac{\alpha}{M} = \text{rpb} \exp\left[1 - \frac{E(1-E)}{y}\,\frac{\partial y}{\partial E}\right]$$

where all quantities on the right-hand side were defined previously for the $F_{0.1}$ criteria. Given the biological parameter m, we can calculate the optimal $F_{0.1}$ criteria and also all quantities in equation (7). Values of $\tilde{\alpha}$ are shown in Fig. 5. Naturally, if the fish stock under study has an $\tilde{\alpha}$ greater than that in equation (7), then the stock is more productive than one in equation (7) and $F_{msy} > F_{0.1}$ and, conversely, $F_{msy} < F_{0.1}$ for a less productive stock.

Maximum sustainable yield is not generally the economic optimum level of fishing. The MSY level is located at the peak of a sustainable yield versus fishing mortality graph that is typically rather flat near the maximum. Thus, MSY (which contains stock–recruitment analysis) suffers the same inefficiency problem that F_{max} exhibits, namely, moving from 99% of MSY to the maximum requires a disproportionate increase in fishing mortality (and effective fishing effort).

By analogy to $F_{0.1}$, let us define the efficient yield F_{ey} criterion for a population at equilibrium as follows:

$$\left.\frac{dY}{dF}\right|_{F=F_{ey}} = (0.1)\left.\frac{dY}{dF}\right|_{F=0}$$

where recruitment can be governed by a stock–recruitment relationship. If recruitment is independent of parent stock abundance, then the F_{ey} criterion simplifies to a $F_{0.1}$ criterion. More generally, I show in Appendix B an equation (B. 4) that characterizes the value of the slope parameter, α for the Ricker curve, where the F_{ey} criterion and optimal $F_{0.1}$ criteria have the same fishing mortality rate when recruitment is governed by a Ricker stock–recruitment function. Those α values are shown in scaled form ($\tilde{\alpha}_{ey} = \alpha/M$) in Fig. 5. Notice in Fig. 5 that $\tilde{\alpha}_{ey} > \tilde{\alpha}_{msy}$ for any given value of m. Therefore, if a stock is more productive (higher α value) than that which causes $F_{msy} = F_{0.1}$, then fishing at $F_{0.1}$ will move the fishery closer to an F_{ey} policy.

In general we can relate the slope of the MSY versus F curve to the optimal $F_{0.1}$ criteria. Let us define the generalized efficient yield F_p value as that value of F where, for a population at equilibrium,

$$\left.\frac{dY}{dF}\right|_{F=F_p} = p\left.\frac{dY}{dF}\right|_{F=0}$$

and again, recruitment can be governed by a stock–recruitment curve. Results similar to the F_{ey} analysis are given in Appendix B which gives equation (B.6) to characterize the value of p where the F_p criterion and optimal $F_{0.1}$ criteria have the same fishing mortality rate for given values of m and $\tilde{\alpha}$. Figure 6 shows the dependence of p on $\tilde{\alpha}$ for $m = 0.5$, 1.5, and 2.5.

The results in this section focus on optimal $F_{0.1}$ criteria. However, the 0.1 factor is somewhat arbitrary and I used it only because of historical precedence. It is a straightforward exercise to substitute another factor for 0.1 throughout this section and the appendices (except in the definition of u given below Appendix B equation (B.5)).

A final note on the theory in this section is appropriate. Optimal $F_{0.1}$ criteria characteristics shown in Fig. 2–6 were numerical approximations. A sieve of size 0.001 was used on my computer to approximate the optimal c and $F_{0.1}$ parameters for values of m iterated by 0.1 from 0.1 to 4.0. The resultant characteristics produced very smooth graphs in some cases (e.g. all of Fig. 6), while others show some chatter. To smooth out numerical noise, I fitted an exponentiated cubic polynomial to the results, which worked very well ($R^2 > 0.99$ in all cases). The smoothed numbers are presented in the figures. The cubic function and parameter values are given in Table 1 so that the reader may compute optimal $F_{0.1}$ parameters more accurately than trying to read them off the figures.

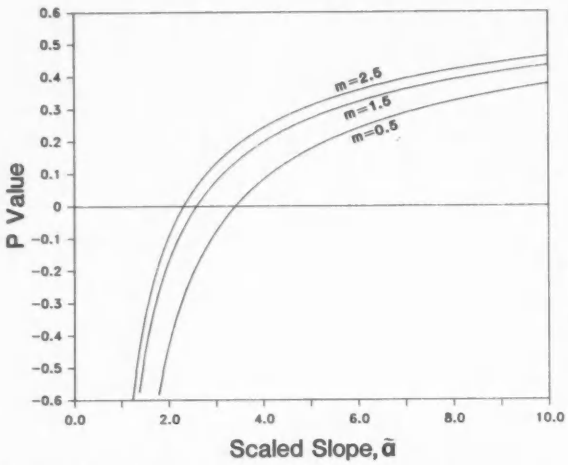

FIG. 6. P values where generalized efficient yield (see text) and $F_{0.1}$ criteria have the same fishing mortality $F_p = F_{0.1}$. The P values are shown as a function of the scaled slope parameter in a Ricker stock–recruitment model $\tilde{\alpha} = \alpha/M$ and for three values of $m = M/K$ (0.5, 1.5, 2.5).

TABLE 1. Polynomial coefficients used to approximate the optimal $F_{0.1}$ criteria parameters listed in the table. Approximation is based on the function $f(m) = \exp(A_0 + A_1m^1 + A_2m^2 + A_3m^3)$ where $m = M/K$ is in the range $0.1 < m < 4$.

Policy parameter	A_0	A_1	A_2	A_3
c_{opt}	−0.072	−0.392	0.063	−0.006
$E_{0.1}$	−0.400	−0.263	0.079	−0.009
$F_{0.1}/M$	0.699	−0.698	0.236	−0.029
c_{opt}/c^*	−0.070	−0.068	0.022	−0.003
$\tilde{\alpha}$ for $F_{msy} = F_{0.1}$	1.549	−0.695	0.232	−0.028
$\tilde{\alpha}$ for $F_{ey} = F_{0.1}$	1.752	−0.709	0.239	−0.029
rpb	0.859	−0.746	0.259	−0.032

Application of Optimal $F_{0.1}$ Theory to Three Fish Stocks

Pacific halibut, western Lake Erie walleye, and Bering Sea Pacific cod stocks were chosen to illustrate application of the $F_{0.1}$ theory. They were selected primarily because estimates of M, K, L_∞, and current (or estimated MSY) fishing mortality were readily available (Table 2). Optimal $F_{0.1}$ parameters are given in Table 3 for data on the three fish stocks in Table 2.

For Pacific halibut, the annual exploitation fraction at MSY is estimated to be $F = 0.22$ based primarily on analysis in Deriso (1985a). The optimal $F_{0.1} = 0.16$ is somewhat lower than the MSY estimate but higher than recent estimates of equilibrium exploitation ($F = 0.14$) given in Deriso (1982). The optimum length of entry (85 cm) is close to the current minimum size limit of 81.5 cm.

Fishing mortality at MSY for western Lake Erie walleye is given in Shuter and Koonce (1987) as $F \approx 0.42$. The optimal $F_{0.1} = 0.29$ is lower than their estimate of F at MSY. Optimum size of entry (0.74 $kg^{1/3}$) corresponds approximately to 3-yr-old fish, whereas Shuter and Koonce's model assumes full selectivity by age 2.

The exploitation fraction recommended in Anomymous (1984b) for Bering Sea Pacific cod is $\mu = 0.4$ ($F = 0.69$) for the 1985 fishery. The optimal $\mu_{0.1} = 0.3$ is lower than their recommended exploitation but higher than their recent estimates of μ for 1979–83, which ranged from 0.04 to 0.14. The optimal size of entry (45 cm) or approximately age 3 Pacific cod is the same age used in Anonymous (1984b) to describe the minimum age of the exploitable stock.

The three optimal $F_{0.1}$ criteria applications all gave exploitation fractions equal to about three fourths of the independent exploitation estimates. MSY estimates are likely to be economically inefficient, as discussed in the previous section, and so optimum rates are likely lower than MSY rates and toward the optimal $F_{0.1}$ criteria. Optimum size of recruitment for the $F_{0.1}$ criteria was very similar to fisheries practice for cod and halibut. It is clear that the walleye is being exploited at too early an age based on the selectivities in Shuter and Koonce's paper, especially since their paper also indicates that walleye do not become sexually mature until age 3.

Discussion

The optimal $F_{0.1}$ criteria are uniquely characterized by the biological parameter m, which is actually a ratio M/K. Methods available for estimating m for a given fish stock range from heavily data-dependent methods (such as M and K are estimated separately then m is computed as the ratio of those two) to a simpler method where m is estimated directly from length frequency data (such as those discussed in this volume by Hoenig et al. 1987) to the simplest methods where K is estimated and then M is predicted based on that K value (e.g. Pauly 1980). Other studies that show that a relationship exists between M and K include Beverton (1963), Beverton and Holt (1959), and Gunderson (1980). Another simple method is given in Alverson and Carney (1975) where an estimate for M is based on the value for K and the oldest age in a stock having at least 0.5% by number of the entire adult stock. It therefore seems likely that a $F_{0.1}$ criterion can be established for essentially all commercially important age-structured stocks. For some stocks, recruitment size is not a management option, and thus, the criterion in this paper may not be useful.

MSY and F_{ey} criteria correspond precisely to F_{max} and $F_{0.1}$ levels of fishing, respectively, when recruitment is independent of parent abundance. When a Ricker stock–recruitment relationship exists, Fig. 5 shows the relationship between optimal $F_{0.1}$ criteria and MSY. Whether or not a manager alters the $F_{0.1}$ criteria because of stock–recruitment depends not only on the presence of a stock–recruitment relationship but also on the amount of stochasticity in that relationship, the manager's time horizon for management, and the manager's degree of risk aversion. Risk here refers to a reluctance on the part of managers to freely gamble with current quotas in an attempt to increase the odds for a higher future catch (e.g. Deriso 1985b). The trade-off we face is between a relatively certain efficient harvest of recruits over their life span with the optimal $F_{0.1}$ criteria (assuming M and K are stable) versus risking a loss of this efficient yield in the hopes that a more optimal recruitment will result in the future from the allowed spawning escapement. We would likely be reluctant to lose the efficient harvest with the optimal $F_{0.1}$ criteria when managing a stock over a moderate time horizon of say 50 yr which exhibited a large degree of randomness in the stock–recruitment process. Indeed, it is likely that the stock–recruitment relationship itself would change over 50 yr given

TABLE 2. Growth and mortality parameter values used to calculate $F_{0.1}$ criteria for Pacific halibut, western Lake Erie walleye, and Bering Sea Pacific cod.

Fish stock	K (yr^{-1})	L_∞	M (yr^{-1})	M/K[d]	Sources
Pacific halibut	0.029[a]	343 cm[a]	0.20	6.90	Deriso 1985a; Deriso and Quinn 1983
Western Lake Erie walleye	0.27[b]	1.06[b]	0.22	0.81	Shuter and Koonce 1988
Bering Sea Pacific cod	0.15[c]	113 cm[c]	0.50	3.33	Anonymous 1984b

[a]Values based on regression of female length data in Deriso (1985a) and females constitute most of the fishable stock.
[b]Values based on regression of the cube root of weight data in reference so that L_∞ units are $kg^{1/3}$.
[c]Values based on regression of combined sex data in reference.
[d]Values based on previous M and K values.

TABLE 3. Optimal $F_{0.1}$ criteria for data in Table 2 along with independent or recommended values of F from sources outside this paper.

Fish stock	$F_{0.1}/M$	$F_{0.1}$	F[a]	$\mu_{0.1}$[b]	c_{opt}	L_{opt}
Pacific halibut	0.81	0.16	0.22	0.14	0.25	85 cm
Western Lake Erie walleye	1.30	0.29	0.42	0.23	0.70	0.74 $kg^{1/3}$
Bering Sea Pacific cod	0.92	0.46	0.69	0.30	0.40	45 cm

[a]Values of F from independent sources. F for halibut is based on MSY in Deriso (1985a); F for walleye is based on MSY in Shuter and Koonce (1988); F for cod is based on recommendation in Anonymous (1984b). See text for further discussion and other values.
[b]Annual exploitation fraction was calculated in the usual manner: $\mu = E(1 - \exp(-Z))$.

that factors affecting survival of the young exhibit serial correlations (e.g. predator abundance, levels of pollution, and other environmental factors).

Risk aversion can also be used to describe a manager's attitude toward the annual variability of catches. For example, fixed escapement policies maximize cumulative catch for a large class of population models (Reed 1979), but at the price of creating a "boom and bust" type fishery. Deriso (1985b) showed that a type of risk averse policy is optimized with a constant exploitation rate for one kind of population model and demonstrated other advantages of such a policy. The $F_{0.1}$ criterion is a constant harvest rate policy and, thus, falls into the type of policy suitable for managers who are risk averse.

In many publications (e.g. Alverson and Pereyra 1969; Gulland 1970), it has been assumed that fishing mortality at MSY equals natural mortality. That assumption has been shown (Francis 1974) to be totally lacking a theoretical basis from the standpoint of a logistic stock production model and also (Deriso 1982) for a more general age-structured model. In this paper, we see, however, that $F \approx M$ is not a bad approximation for optimal $F_{0.1}$ criteria when $1 < m < 4$. But there is no need to rely on that approximation, since we can just as easily find the precise ratio of F to M for optimal $F_{0.1}$ criteria in Fig. 4. It is important to note that support of the $F \approx M$ approximation in a constant harvest rate policy does *not* imply that a reasonable policy would be to fix catch at a level equal to $0.5 \cdot m \cdot$(virgin stock biomass), the equivalent to $F = M$ for a logistic model at equilibrium; Beddington and Cooke (1983) argued against such a fixed catch policy.

We should be able to adapt the optimal $F_{0.1}$ criteria to a multispecies framework and a changing environment. One approach would be to allow both M and K to be slowly varying functions of time so that m slowly changes in time. This would allow us to update the optimal $F_{0.1}$ values as m changes and thus adapt the criteria to changing environmental and biological conditions. I emphasize the Ricker stock–recruitment function in this paper only because I use it for Pacific halibut (Deriso 1985a); results could be generalized for other stock–recruitment functions. These should make interesting topics for further research.

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Glossary of Key Parameters

α = parameter of the Ricker stock–recruitment function

$\tilde{\alpha}$ = α/M = scaled parameter of the Ricker stock–recruitment function

$\tilde{\alpha}_{ey}$ = value of $\tilde{\alpha}$ where the optimal $F_{0.1}$ criteria and the F_{ey} policy have the same fishing mortality rate

$\tilde{\alpha}_{msy}$ = value of $\tilde{\alpha}$ where the optimal $F_{0.1}$ criteria and MSY have the same fishing mortality rate

B = average biomass of the fishable stock at equilibrium

β = parameter of the Ricker stock–recruitment function

c = length of fish at recruitment age divided by maximum (asymptotic) length

c^* = critical size, which is the value of c where biomass of a cohort is maximum in the absence of fishing

c_{opt} = value of c that maximizes yield when fishing mortality rate is fixed at the $F_{0.1}$ value

E = $F/(F + M)$ = rate of exploitation

$E_{0.1}$ = value of E evaluated at the $F_{0.1}$ fishing mortality rate

F = annual fishing mortality rate

$F_{0.1}$ = fishing mortality rate, as defined by equation (5), where marginal yield per recruit is 10% of the marginal yield per recruit with little fishing

F_{msy} = fishing mortality rate that produces MSY for a population with both a Ricker stock–recruitment relationship and age-structured growth and mortality (as specified in a Beverton and Holt year-class model)

F_{ey} = similar age-structure dynamics as in F_{msy}, except that this fishing mortality rate is where marginal equilibrium yield is 10% of the marginal equilibrium yield in a lightly exploited stock

F_p = similar age-structure dynamics as in F_{msy}, except that this fishing mortality rate is where marginal equilibrium yield is p times the marginal equilibrium yield in a lightly exploited stock

K = parameter of the von Bertalanffy length equation

L_c = length of fish at age of recruitment

L_∞ = asymptotic length and a parameter of the von Bertalanffy length equation

M = annual natural mortality rate

m = M/K = ratio of natural mortality rate to von Bertalanffy growth rate parameter

$N(t_0)$ = abundance of a year-class at hypothetical age t_0

R = abundance of a year-class when they reach recruitment length L_c

rpb = recruitment biomass as a fraction of fishable stock biomass, all divided by natural mortality rate

t^* = critical age corresponding to size c^*

t_w = average age of biomass in the fishable stock

t_c = recruitment age

μ = annual exploitation fraction, $E\,[1 - \exp(-M - F)]$

W_∞ = asymptotic weight parameter

Y = total yield taken from a year-class

Y' = total yield as a fraction of RW_∞, recruitment abundance times asymptotic weight

y = total yield as a fraction of $N(t_0)\,W_\infty$

y^* = maximum value of y, as derived in equation (4)

Appendix A. Derivation of Necessary Conditions for $F_{0.1}$ to Equal F_{msy}

Let us assume that recruitment biomass is determined by average fishable adult biomass according to the Ricker stock–recruitment curve

$$B(t_c) = G(B) = \alpha B \exp(-\beta B)$$

where average adult biomass (B) is calculated as

$$B = \int_{t_c}^{\infty} B(x)dx$$

for the population at equilibrium. Total yield Y at equilibrium can be written as

$$Y = (\mathrm{YPR})B(t_c)$$

where YPR is defined as the yield per recruit biomass at equilibrium. A necessary condition for MSY is

$$\text{(A.1)}\quad \frac{dY}{dF} = 0$$

which implies that

$$\frac{d\mathrm{YPR}}{dF} = \frac{-\mathrm{YPR}}{B(t_c)}\,\frac{dB(t_c)}{dF}.$$

By the chain rule,

$$\frac{dB(t_c)}{dF} = \frac{dG(B)}{dB}\,\frac{dB}{dF}.$$

Since

$$Y = FB$$

then

$$\frac{dY}{dF} = 0$$

implies

$$\frac{dB}{dF} = \frac{-B}{F}$$

which can be substituted above to get

$$\text{(A.2)}\quad \frac{dB(t_c)}{dF} = \frac{-B}{F}\,\frac{dG(B)}{dB}.$$

At equilibrium,

$$B = \frac{1}{\mathrm{RPB}}\,G(B)$$

where RPB is the recruit production fraction $(B(t_c)/B)$. For a Ricker curve this means that equilibrium adult average biomass can be written as

$$B = \ln(\alpha/\mathrm{RPB})/\beta$$

and thus

$$\frac{dG(B)}{dB} = (1 - \beta B)\alpha e^{-\beta B} = \mathrm{RPB}(1 - \ln(\alpha/\mathrm{RPB})),$$

and combining the above expression with (A.1) and (A.2) implies

$$\text{(A.3)}\quad \frac{d\mathrm{YPR}}{dF} = \frac{\mathrm{YPR}}{F}(1 - \ln(\alpha/\mathrm{RPB})).$$

For the simple yield theory of equation (2), we can construct an equivalent condition for MSY in terms of relative yield (y). Since

$$\mathrm{YPR} = \frac{Y}{B(t_c)} = \frac{Y}{W_\infty N_0(1-c)^m c^3} = \frac{y}{(1-c)^m c^3},$$

we see that equation (A.3) can be written as

$$\frac{dy}{dF} = \frac{y}{F}(1 - \ln(\alpha/\mathrm{RPB}))$$

or in terms of the exploitation rate, $E = F/(F + M)$, and scaled recruit production fraction, $\mathrm{rpb} = \mathrm{RPB}/M$,

$$\frac{dy}{dE} = \frac{y}{E(1-E)}(1 - \ln(\alpha/M) + \ln(\mathrm{rpb})).$$

Solving for (α/M), we find

$$\text{(A.4)}\quad \frac{\alpha}{M} = \mathrm{rpb}\exp\left[1 - \frac{E(1-E)}{y}\,\frac{dy}{dE}\right].$$

All quantities in the right-hand side of equation (A.4) can be calculated for a given $F_{0.1}$ criterion. Substitute those calculated quantities into (A.4) to find the scaled recruit slope parameter. α/M, necessary for $F_{msy} = F_{0.1}$.

Appendix B. Derivation of Necessary Conditions for $F_{0.1}$ to Equal F_{ey}

This derivation uses the same definitions and assumptions as Appendix A, except here our objective to characterize α/M values where $F_{0.1} = F_{ey}$. The efficient yield is defined as that yield, where for a population at equilibrium,

$$\text{(B.1)}\quad \left.\frac{dY}{dF}\right|_{F=F_{ey}} = (0.1)\left.\frac{dY}{dF}\right|_{F=0},$$

and where recruitment is determined by a stock–recruitment curve. Total yield at equilibrium can be written as $Y = \mathrm{YPR}\,B(t_c)$ and, thus,

$$\text{(B.2)}\quad \frac{dY}{dF} = \frac{d(\mathrm{YPR})}{dF}B(t_c) + \mathrm{YPR}\,\frac{dB(t_c)}{dF}.$$

This latter derivative can be written as $dB(t_c)/dF = (dG)(B)/(dB)(dB/dF)$ to get

$$\text{(B.3)}\quad \frac{dB(t_c)}{dF} = [1 - \ln(\alpha/\mathrm{RPB})][dY/dF - B]/\mathrm{YPR}$$

since

$$\frac{dG(B)}{dB} = \mathrm{RPB}[1 - \ln(\alpha/\mathrm{RPB})]$$

for the Ricker stock–recruitment curve and since

$$Y = \mathrm{FB}$$

implies

$$\frac{dY}{dF} = F\,\frac{dB}{dF} + B.$$

Substitute (B.3) into (B.2) along with the equilibrium value for $B = \ln(\alpha/\mathrm{RPB})/\beta$ and simplify the expression to get

$$\frac{\mathrm{RPB}}{\beta}\,\frac{d\mathrm{YPR}}{dF} - \frac{1}{\beta} - \frac{dY}{dF} + B = 0,$$

which we evaluate at $F = F_{ey}$, and substitute this answer into (B.1) (and after considerable algebra) to get

$$\text{(B.4)}\quad \frac{\alpha}{M} = \exp\left[\frac{V - 1 + v\ln(\mathrm{rpb}_0) - \ln(\mathrm{rpb}_1)}{v - 1}\right]$$

where $v = \mathrm{RPB}\,(0.1)\,(d\mathrm{YPR}/dF)$ evaluated at $F = 0$, $V = \mathrm{RPB}\,(d\mathrm{YPR}/dF)$ evaluated at $F = F_{ey}$, $\mathrm{rpb}_0 = \mathrm{RPB}/M$ evaluated at $F = 0$, and $\mathrm{rpb}_1 = \mathrm{RPB}/M$ evaluated at $F = F_{ey}$.

As in Appendix A, we make a change of variables to $E = F/(F + M)$ and $y = (1 - c)^m c^3\,\mathrm{YPR}$ to rewrite (B.4) as

$$\text{(B.5)}\quad \frac{\alpha}{M} = \exp\left[\frac{v - 1 + u\ln(\mathrm{rpb}_0) - \ln(\mathrm{rpb}_1)}{u - 1}\right]$$

where

$$u = \mathrm{rpb}_0\,\frac{(1 - E)^2}{(1 - c)^m c^3}\,(0.1)\,\frac{dy}{dE}$$

evaluated at E = 0 and

$$v = \mathrm{rpb}_1\,\frac{(1 - E)^2}{(1 - c)^m c^3}\,\frac{dy}{dE}$$

evaluated at $E = E_{ey}$. All quantities in the right-hand side of equation (B.5) can be calculated for a given $F_{0.1}$ criterion. Substitute those calculated quantities into (A.4) to find the scaled recruit slope parameter, α/M, necessary for $F_{ey} = F_{0.1}$.

Equation (B.5) can be easily modified to characterize conditions for an equilibrium yield and fishing mortality (defined here as F_p) where

$$\left.\frac{dY}{dF}\right|_{F=F_p} = p\left.\frac{dY}{dF}\right|_{F=0}$$

for any given fraction p, rather than the fixed (0.1) in equation (B.1). The scaled slope parameter is found in equation (B.5) where we only need to change the (0.1) factor to (p) in the definition of u given above and where v and rpb_1 are evaluated for $F = F_p$.

For a given slope, α/M, we can also calculate the corresponding p which causes $F_p = F_{0.1}$, the (0.1) fishing mortality calculated from yield per recruit theory. Solve for u in (B.5) to get

$$\text{(B.6)}\quad u = \frac{\ln(\alpha/M) + v - 1 - \ln(\mathrm{rpb}_1)}{\ln(\alpha/M) - \ln(\mathrm{rpb}_0)}$$

from which p is easily calculated. We substitute a given value for α/M and the quantities calculated for the $F_{0.1}$ criteria into the right-hand side of (B.6) and the defining equation of u given below equation (B.5).

Use of a Mixed-Species Yield-per-Recruit Model to Explore the Consequences of Various Management Policies for the Oregon Flatfish Fishery[1]

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Pikitch, E. K. 1987. Use of a mixed-species yield-per-recruit model to explore the consequences of various management policies for the Oregon flatfish fishery. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 349–359.

A mixed-species yield-per-recruit model is developed for a portion of the Oregon flatfish fishery. The model is applied to examine the effects of implementing various management policies on fishery yield in weight and revenues for Pacific Marine Fisheries Commission Area 2B. Three types of management policies are considered: maximization of output, efficiency-oriented, and a minimum trawl cod-end mesh size regulation with no restriction of effort. If an efficiency-oriented policy were adopted, the current minimum mesh size regulation of 114 mm would be optimal. However, if effort is left unrestricted, or if a maximization strategy were adopted, a larger mesh size would result in greater volume yields. Optimal mesh size is more sensitive to the management policy selected than it is to either variations in recruitment or to costs associated with fishing. If economic considerations become more important in formulating management policy, greater gains could be achieved by limiting effort than by altering mesh size regulations. However, as the management policy becomes less restrictive of effort, the influence of mesh size on fishery output increases.

Un modèle de rendement par recrue polyvalent a été mis au point pour une partie de la pêche du poisson plat de l'Oregon. Le modèle vise à examiner les effets de diverses politiques de gestion sur le rendement des pêches au niveau du poids et des revenus pour la zone 2B de la Commission des pêches maritimes du Pacifique. Trois types de politiques de gestion sont envisagés : maximalisation de la production, accent sur l'efficacité et règlement sur le maillage minimal du cul-de-chalut sans limitation de l'effort de pêche. Si on adoptait une politique axée sur l'efficacité, le maillage minimal actuel de 114 mm ne pourrait être dépassé. Toutefois, si l'effort de pêche n'est pas réglementé ou si une politique de maximalisation des prises était adoptée, l'augmentation du maillage donnerait des prises plus élevées. Le maillage maximal est davantage fonction de la politique de gestion adoptée que des fluctuations du recrutement ou des coûts liés à la pêche. Si les questions économiques devaient importer encore plus dans la formulation d'une politique de gestion, on obtiendrait de meilleurs gains en limitant l'effort de pêche plutôt qu'en modifiant le règlement sur le maillage. Toutefois, le maillage influe davantage sur l'importance des prises à mesure que la politique de gestion devient moins restrictive relativement à l'effort de pêche.

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It has long been recognized that when species interact biologically and/or are susceptible to fishing by a common gear, it is generally not possible to manage each species at its optimum level (Beverton and Holt 1957; Anderson 1975; Pope 1979; May et al. 1979; Mitchell 1982). Although tools for analyzing the aggregate yield of mixed-species fisheries have been available for some time, their application has proceeded rather slowly. For example, in an early treatise, Beverton and Holt (1957, p. 422) derived a eumetric curve for an aggregate of species subject to technological interactions. Recognizing that a given amount of fishing effort (f) may result in different levels of fishing mortality (F_i) for each species i, they developed an index, I, for which a value of 1.0 represented the pre-war values of F_i, $I = 0.5$ equalled half the pre-war values of F_i, and so on. They then referred back to the yield–isopleth plots for each species and, after weighting the yield of each species by its respective price, derived an aggregate eumetric curve for revenues in terms of I.

Despite the early availability of Beverton and Holt's example, mixed-species yield-per-recruit analyses appear to have gone virtually unused. However, Murawski (1984) recently provided a detailed account of a single-fishery mixed-species yield-per-recruit model which is quite similar conceptually to that presented by Beverton and Holt. Murawski also extended the model to examine the case where several fisheries exploit

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differing mixtures of the same stocks and applied both the single and multiple fishery models to the Georges Bank otter trawl fishery.

In this paper I describe a mixed-species yield-per-recruit model for a segment of the Oregon groundfish fishery which incorporates elements of both the Beverton–Holt and Murawski approaches. The model is then used to explore the consequences of variations in fishing effort and mesh size on both biological and economic yields from the fishery. The segment of the fishery that is examined is the otter trawl fishery which employs "sole gear" and which exploits primarily three species of flatfish: Dover sole (*Microstomus pacificus*), English sole (*Parophrys vetulus*), and petrale sole (*Eopsetta jordani*). Although other species of fish are caught in the sole fishery, my analysis is limited to these three species because data required to include the others are not available. However, because Dover, English, and petrale sole have comprised the major portion of sole gear landings since the inception of the fishery, it is unlikely that inclusion of these ancillary species would significantly alter the implications of these analyses to overall fisheries management policy. Similarly, some Dover, English, and petrale sole are retained by other gear types, but the fraction of landings accounted for by alternate gear types is minor.

The Oregon flatfish fishery is managed by the Pacific Fishery Management Council (PFMC) under the Pacific Coast Groundfish Plan (PFMC 1982) and its amendments. Current regulations include a minimum mesh size of 4.5 in. (114 mm). Although quotas have not been used in the management of flatfish, determinations of "Allowable Biological Catches" (ABC's; desirable harvest levels) are made and are updated as needed (Lenarz 1979; Demory 1984a, 1984b; Demory et al. 1984). To date, the assessments of ABC's for Dover, English, and petrale sole have been based largely on the concept of maximum sustained yield (MSY) in weight, and have been determined via single-species analyses.

In a review of the Pacific Coast Groundfish Plan, Huppert (1985) concluded, in part, that there is room for improvement in incorporating "multispecies considerations and non-biological objectives in setting levels of optimum yield." The model presented herein provides an analytical tool for incorporating multispecies considerations into the assessment of one segment of the Pacific Coast groundfish fishery. The model is then used to explore optimal mesh regulations under alternative management policy objectives.

Model Structure

The model accounts for the fact that the three species are technologically interrelated in that they are caught together in individual trawl hauls. However, the model does not address biological interactions among the species. Food habits studies indicate that any biological interactions that may occur among these species are probably small. The diet of the petrale sole is quite distinct from that of the other two species, as it feeds largely on pelagic prey, including shrimp, euphausiids, cephalopods, and fish (Ketchen and Forrester 1966; Pearcy and Vanderploeg 1973; Kravitz et al. 1977; Wakefield 1984). English and Dover sole are primarily benthophagus, feeding on a wide variety of epifaunal and infaunal invertebrates, and have been described as opportunistic feeders (Kravitz et al. 1977; Pearcy and Hancock 1978; Hogue and Carey 1982; Wakefield 1984). Although Dover and English sole feed on the same general types of prey, diet overlap among these species is generally low (Wakefield 1984), and they have been described as belonging to different feeding guilds (Allen 1982).

The model is based on the assumption that recruitment is constant, but allows for differences by species and sex. Recruitment is defined as the number of fish of age r, where r is the youngest age that is at least partially susceptible to retention by the smallest mesh size considered. Previous work has indicated that for some species of flatfish, recruitment is nearly independent of stock size over a wide range of exploitation rates (Cushing 1971; Cushing and Harris 1973). Spawning time, recruitment, and growth of Dover and English sole have been shown to vary with changing environmental conditions, but not with respect to stock abundance (Hayman and Tyler 1980; Kreuz et al. 1982; Kruse and Tyler 1983).

The model accounts for species-, sex-, and age-specific differences in catchability, growth, mortality, discard rate, and value. Following Murawski (1984), instantaneous fishing mortality rate is assumed to be directly proportional to fishing effort. It is further assumed that all fish that are caught die, regardless of whether they are discarded at sea or retained. According to Saila (1983) the latter assumption is reasonable for temperate-water otter trawl fisheries.

Although parameter values differ, the calculations that are performed for each species, sex, and mesh size are identical. For improved readability, use of subscripts has been limited to that denoting age in the next section.

For each age t, length at age, l_t, is calculated via the von Bertalanffy equation:

$$l_t = L_\infty(1 - \exp(-K(t - t_0)))$$

where L_∞, K, and t_0 are model input parameters. The value of l_t so derived is then used to calculate individual weight at age, w_t, via the formula

$$w_t = a \cdot l_t^b$$

where a and b are input constants.

For a given quantity of fishing effort, f, the model calculates the instantaneous fishing mortality rate for age groups that are fully vulnerable to the gear:

$$F = q \cdot f$$

where q is the catchability coefficient. Weight caught, WC, is computed according to the catch equation

$$\mathrm{WC} = \sum_t \mathrm{WC}_t = \sum_t \left[N_t \cdot \frac{(F \cdot \mathrm{PR}_t)}{(F \cdot \mathrm{PR}_t + M)} \times [1 - \exp[-(F \cdot \mathrm{PR}_t + M)] \cdot w_t \right]$$

where N_t = number of fish age t, PR_t = fraction of age t fish retained by the gear, and M = instantaneous natural mortality rate. The product $F \cdot \mathrm{PR}_t$ is only an approximation of the actual age-specific instantaneous fishing mortality rate, since as defined, PR_t is not a direct multiplier of an instantaneous rate. However, Murawski (1984) claimed that sensitivity analyses indicated that it provided useful estimates of actual values, particularly for moderate ranges of PR_t and F.

The numbers of recruits, N_r, is an input parameter. Numbers of fish in the population of ages older than the age of recruitment are determined by the recursive formula

$$N_{t+1} = N_t \cdot [\exp(-(M + F \cdot \mathrm{PR}_t))].$$

Landed weight is calculated as

$$\mathrm{WL} = \sum_t \mathrm{WL}_t = \sum_t [\mathrm{WC}_t \cdot (1 - \mathrm{FD}_t)]$$

TABLE 1. Parameter estimates used in implementing the mixed-species yield-per recruit model.

Parameter	Dover sole		English sole		Petrale sole	
	Male	Female	Male	Female	Male	Female
Von Bertalanffy constants[a]						
L_∞	40.5	50.4	36.3	42.6	45.4	54.4
K	0.094	0.094	0.256	0.265	0.202	0.212
t_0	−1.55	−2.18	−1.08	−0.4	0.08	−1.82
Length–weight coefficients[a]						
a	0.0134	0.0101	0.0078	0.0022	0.0040	0.0030
b	2.8911	2.9655	3.0132	3.4003	3.3760	3.2812
1985 ex-vessel price ($/kg)[b]	0.55	0.55	0.75	0.75	1.65	1.65
Minimum market length (cm)[b]	34.0	34.0	31.0	31.0	33.0	33.0
M[a]	0.15	0.15	0.26	0.26	0.25	0.20
F(1971–74 average, PMFC Area 2B)[c]	0.15	0.15	0.21	0.21	0.43	0.43
$q \times 10^{-3}$[d]	0.01568	0.01568	0.02195	0.02195	0.04495	0.04495
Number of recruits (millions)[e]	10.94	13.56	0.78	5.44	3.76	2.33
Age of recruitment[e]	5	5	1	1	1	1

[a]Data for Dover, English, and petrale sole were obtained, respectively, from Demory et al. (1984), Demory (1984a) and Demory (1984b). Length–weight coefficients are for an equation of the form $W = aL^b$ where L is length (cm) and W is weight (g).
[b]P. Leipzig (pers. comm.).
[c]Demory et al. (1976).
[d]q is derived by dividing F by average number of trawling hours conducted in PMFC Area 2B during 1971–74 (i.e. 9566 h).
[e]See text for explanation.

where FD_t is the fraction of age t fish discarded dead at sea. Gross revenues, GR, are determined by the equation

$$GR = \sum_t GR_t = \sum_t [WL_t \cdot p_t)$$

where p_t = ex-vessel price per unit weight. Note that $p_t = 0$ for fish that are smaller than the minimum market length.

Let subscripts i and j denote species i and sex j. Total weight caught for the aggregate of all species and sexes is then

$$TWC = \sum_i \sum_j WC_{ij},$$

total weight landed, TWL, is

$$TWL = \sum_i \sum_j WL_{ij},$$

total gross revenues, TGR, are

$$TGR = \sum_i \sum_j GR_{ij},$$

and total net revenues, TNR, are

$$TNR = TGR - c \cdot f$$

where c = operating costs per unit of fishing effort. Note that it has been assumed that total operating costs are proportional to effort, and the model does not discriminate between fixed and variable costs. These were necessary simplifying assumptions of the analysis. In reality, the marginal costs of a unit of fishing effort may be relatively low until an additional vessel is needed to achieve the next effort level. Thus, rather than being linear, the relationship between effort and costs may be a step function.

Model Application

Parameter Estimation

Biological parameter estimates used in the model and their sources are given in Table 1. Data on length-specific at-sea discard rates were taken from TenEyck and Demory (1975) and are presented in Table 2. Length-specific gear retention rates for each species and mesh size were estimated from data published by Best (1961). Best's experiments were conducted using nets constructed of cotton twine, whereas most vessels now use nylon-thread nets. However, data on selectivity of modern gear were not available, and it was therefore necessary to assume that the selectivity properties of modern gear are similar. Best's data from experiments conducted using similar mesh sizes were averaged and smoothed and the resulting length-specific retention rates were then assigned to mesh categories which were

TABLE 2. Length-specific discard rates for three species of flatfish. Data are from TenEyck and Demory (1975).

Length (cm)	Percent discarded at Sea		
	Dover sole	English sole	Petrale sole
18	100	100	100
19	100	100	99
20	100	100	99
21	100	94	98
22	100	88	97
23	100	82	96
24	99	76	95
25	95	69	93
26	92	62	91
27	88	55	89
28	85	47	87
29	80	40	84
30	75	34	81
31	70	29	73
32	65	24	65
33	61	20	57
34	56	15	50
35	50	11	43
36	43	8	36
37	36	6	29
38	26	5	23
39	16	4	18
40	11	3	14
41	8	1	10
42	5	0	7
43	3	0	4
44[a]	1	0	2

[a]Discard rates for fish of all species greater than 44 cm are zero.

named to reflect (approximately) the average mesh sizes used. This yielded four mesh categories: 102 mm (4.0 in.), 114 mm (4.5 in.), 127 mm (5.0 in.), and 140 mm (5.5 in.) (Table 3).

Because catchability coefficients and stock-specific recruitment levels vary in different areas of the Pacific Coast, the model was implemented for a single area to illustrate its use. The area is PFMC Statistical Area 2B, located off the coast of southern Oregon, and is bounded by Cape Perpetua on the north and Cape Blanco on the south. It includes a major fishing port at Coos Bay, traditionally accounting for a large proportion of Oregon's groundfish landings. In addition, flatfish have comprised the largest fraction of groundfish landings at Coos Bay (Oregon Department of Fish and Wildlife (ODFW), unpubl. data).

Direct estimates of instantaneous fishing mortality rates (F_i) for each species during 1971–74 were available as a result of surveys conducted by the ODFW (Demory et al. 1976). To obtain estimates of species-specific catchability coefficients, values of F_i were divided by the average number of annual trawling hours in Area 2B during 1971–74 (ODFW, unpubl. data; Table 1).

Recall that for a population in equilibrium with a given level of F, and for which recruitment is constant, landings of that population in a given year are equal to the equilibrium yield of a cohort during its lifetime (Beverton and Holt 1957, p. 38). Thus, under equilibrium conditions, an estimate of recruitment (N_r) can be derived by dividing actual landings by landings-per-recruit that would be expected under the specified age at entry and fishing mortality rate.

The trawl fishery operating in Area 2B during the early 1970's was characterized by fairly stable fishing intensity. Effort, as measured by annual trawling hours, ranged from 8492 h in 1974 to 11 229 h in 1972 and averaged 9566 h from 1971 to 1974 (ODFW, unpubl. data). Assuming that relatively stable fishing intensity resulted in constant fishing mortality rates, then the requirement of equilibrium conditions can be assumed.

Estimates of yield per million recruits were obtained by running the model separately for each species at an effort level of 9566 h with observed age at entry and fishing mortality rate and with N_r set at 10^6 recruits. The estimates of landed weight resulting from the model run for the 114-mm mesh (corresponding to the 4.5-in. minimum mesh size restriction in effect) were then multiplied by 10^{-6} to obtain an estimate of landed weight-per-recruit for each species and sex. Actual landed weights were then divided by their respective estimates of landed weight per recruit to obtain estimates of recruitment for each species and sex (Table 1).

Minimum acceptable market lengths and ex-vessel prices for each species and sex were taken from market orders issued by the Fishermen's Marketing Association (FMA) (Table 1; P. Leipzig, FMA, 320 Second St., Suite 2-B, Eureka, CA 95501, pers. comm.). Although acceptable lengths and ex-vessel prices differ among processing plants, many vessels in Oregon are members of FMA, and hence, FMA averages are representative of industry-wide figures. Average operating costs per trawling hour were estimated by weighting operating costs for boats belonging to different size categories by the amount of fishing effort expended annually by boats in each category (Table 4), yielding an estimate of $36.42 per trawling hour. This gives an aggregated estimate of both fixed and variable costs, and hence may not reflect the actual cost of a marginal unit of effort.

Management Policy Options

The Groundfish Management Plan defines optimum yield as "all the fish that are landed under regulations adopted by the Council." This definition does not provide much insight into management objectives, but according to Huppert (1985), current practice is to attempt to obtain MSY of each managed species or species group. However, an MSY policy can lead to decreased population stability and is often economically inefficient (Larkin 1977). It is therefore of interest to determine the sensitivity of equilibrium fishery outputs and optimal mesh sizes under alternative management policies. For the mixed-species aggregate, three kinds of equilibrium fishery outputs are considered: marketable weight (yield), gross revenues, and net revenues. The six management policies examined differ in their objectives and in the type of fishery controls employed and fall into three general categories as follows.

Maximization of fishery output (MSY and MGR)

The policy which seeks to maximize equilibrium yield using both effort and mesh size as fishery controls will be denoted as MSY. Because it is highly unlikely that the individual species yields will each be maximized at the same level of effort and mesh size, this aggregate species MSY will be smaller than the sum of the MSY's for the individual species. In addition, because the species under consideration differ greatly in value, the level of effort for which MSY is achieved will not necessarily coincide with that at which gross revenues are maximum. The policy which seeks to maximize gross revenues, again using mesh size and effort as controls, will be denoted as MGR.

TABLE 3. Gear selectivity coefficients by species and mesh size. Data are from Best (1961).

Length (cm)	Percent retained by species and mesh size (mm)											
	Dover sole				English sole				Petrale sole			
	102	114	127	140	102	114	127	140	102	114	127	140
18	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	60	0	0	0
22	0	0	0	0	15	7	8	0	100	30	0	0
23	0	0	0	0	30	11	8	0	100	100	10	0
24	0	0	0	0	45	15	9	0	100	100	20	0
25	0	0	0	0	62	20	10	0	100	100	30	0
26	0	0	0	0	96	28	13	0	100	100	40	0
27	0	0	0	0	100	33	17	0	100	100	50	9
28	15	0	0	0	100	36	23	13	100	100	65	18
29	24	0	0	0	100	55	36	18	100	100	87	28
30	42	19	0	0	100	71	48	23	100	100	97	42
31	59	25	1	0	100	78	57	25	100	100	100	62
32	70	38	2	0	100	82	66	30	100	100	100	83
33	83	44	3	0	100	85	74	35	100	100	100	96
34	91	52	5	0	100	88	83	40	100	100	100	100
35	98	62	8	1	100	91	88	47	100	100	100	100
36	100	74	14	1	100	94	92	58	100	100	100	100
37	100	89	21	1	100	97	95	70	100	100	100	100
38	100	95	29	2	100	99	97	81	100	100	100	100
39	100	99	39	2	100	100	99	89	100	100	100	100
40	100	100	53	4	100	100	100	95	100	100	100	100
41	100	100	66	5	100	100	100	98	100	100	100	100
42	100	100	77	7	100	100	100	100	100	100	100	100
43	100	100	88	10	100	100	100	100	100	100	100	100
44	100	100	97	14	100	100	100	100	100	100	100	100
45	100	100	100	18	100	100	100	100	100	100	100	100
46	100	100	100	23	100	100	100	100	100	100	100	100
47	100	100	100	30	100	100	100	100	100	100	100	100
48	100	100	100	45	100	100	100	100	100	100	100	100
49	100	100	100	65	100	100	100	100	100	100	100	100
50	100	100	100	90	100	100	100	100	100	100	100	100
51[a]	100	100	100	100	100	100	100	100	100	100	100	100

[a]Fish of all species that are greater than 51 cm are assumed to be fully retained by all mesh sizes.

Efficiency-oriented strategies (MNR and $f_{0.1}$)

From an efficiency standpoint, it is not usually desirable to manage for maximum output, because the rate of increase in output decreases while the costs of obtaining that output continue to increase prior to the attainment of maximum output (i.e. a point of diminishing returns to effort is reached). A policy which seeks to maximize net revenues from the fishery (MNR policy), while potentially producing smaller yields or gross revenues than the maximization policies, results in a more efficient use of effort. To consider efficiency when weight is the output variable of interest, an $f_{0.1}$ policy is examined. Both MNR and $f_{0.1}$ policies are analyzed using mesh size and effort as controls.

An $f_{0.1}$ policy is analogous to an $F_{0.1}$ policy for single species (e.g. Deriso 1987). For a given mesh size, such a policy would restrict fishing effort to a level at which the marginal equilibrium marketable yield in weight resulting from an additional unit of effort is one-tenth the marginal equilibrium yield at very low levels of fishing (Gulland 1983).

Mesh size only policies (MSO policies, MSOY, MSOGR)

According to static equilibrium economic theory (Gordon 1953, 1954), when there are no restrictions on entrance into a fishery, effort will tend to stabilize at a level where there are no net revenues generated from the fishery. Thus, if a mesh size regulation is the only control applied to a fishery, no net revenues but some yield and gross revenues would be obtained at equilibrium. The level of effort at which zero net revenues occurs will differ for different mesh sizes, as will the amount of yield and gross revenues generated. Thus, it is possible to select a mesh size that maximizes yield at the point of zero net revenues. Except by extraordinary coincidence, the resultant yield would be less than that which would be obtained under an MSY policy, in which both effort and mesh size are controlled. I denote the policies that seek to maximize yield or gross revenues using mesh size as the only fishery control by MSOY and MSOGR, respectively.

Optimal Mesh Size

For each mesh size m_i, there is a unique level of effort f_i that would result from the implementation of a given management policy. For the maximization and efficiency-oriented policies the value of f_i is set by regulation, whereas for the MSO policies

TABLE 4. Data used to estimate operating costs per trawling hour for the Oregon flatfish trawl fleet.[a]

	Boat category		
	Small (9.0–14.9 m)	Medium (15.0–21.0 m)	Large (21.1–27.1 m)
(1) Number of trips per year	398	630	464
(2) Days fished per trip	2.21	2.21	2.29
(3) Days running per trip	0.84	1.06	1.21
(4) Days out per trip	3.05	3.27	3.50
(5) Hours fished per year	21 110	33 415	25 501
(6) Operating cost per day out ($)	500	588	675
(7) Annual operating expenditures ($)	606 950	1 211 339	1 096 200
(8) Cost per hour fished ($)	28.75	36.25	42.99

SOURCES: (1), (2), and (3), Johnson et al. 1982 (table 5, p. 8); (4) = (2) + (3); (5) = (1) × (2) × 24; (6) Swartzman et al. 1985 (table 7); (7) = (1) × (4) × (6); (8) = (7)/(5).

[a]Average cost per trawling hour is derived by dividing the sum of the numbers in row 7 by the sum of numbers in row 5.

it occurs without intervention and at a level at which net revenues are zero. Further, for each management policy there is a particular yield characteristic (e.g. marketable weight, gross revenues, etc.) that is of interest. One can define the optimal mesh size for a given management policy as the mesh size that produces the maximum equilibrium level of the yield characteristic of concern at effort level f_i. This is a generalized form of the definition given by Deriso (1987) for optimal age-at-entry for an $F_{0.1}$ policy.

To illustrate, under a MNR policy, the yield characteristic of concern is net revenues. A strict implementation of that policy for a given mesh size, m_i, would result in restricting effort to the level f_i at which net revenues are maximum (MNR_i). Four values of MNR_i can be generated, corresponding to the four mesh sizes under consideration. Thus, the optimal mesh size under a MNR policy is

$$m_{\text{opt, MNR}} = m_j \text{ such that } MNR_j = \max\{MNR_i, i = 1, 4\}.$$

Proceeding in this way for each management policy being considered, a series of optimal mesh sizes can be generated. The choice of a single optimum mesh size for management purposes will depend on the definition of optimum yield that is adopted.

Results

Optimal Mesh Size under Alternative Management Policies

For both maximization policies (MSY and MGR), the optimal mesh size is 127 mm, a mesh size larger than the current 114-mm mesh size regulation now in effect (Table 5). Maximum yields for the MSY policy with 114- and 102-mm mesh sizes are, respectively, 93 and 83% of that obtainable with the optimal mesh. Similarly, for the MGR policy, maximum gross revenues for 114- and 102-mm mesh sizes are both within 95% of the maximum gross revenues for the 127-mm mesh.

For the efficiency-oriented policies (MNR and $f_{0.1}$), the optimal mesh size falls to 114 mm (Table 5). However, net revenues are much more sensitive to variations in effort than to variations in mesh size (Fig. 1). A mesh size of 127 mm could provide 97% of the MNR and 97% of the $f_{0.1}$ level of yield associated with the 114-mm mesh. Similarly, the smallest mesh size could provide 97% of MNR and 92% of the $f_{0.1}$ level of yield of the 114-mm mesh. Thus, if a maximization or efficiency-oriented management strategy is adopted, it makes little difference which mesh size is used, because three of the four mesh sizes considered will provide similar yields and revenues. However, the results indicate that use of the largest mesh (140 mm) would significantly reduce yields, regardless of which of these management policies is chosen.

Each of the aforementioned policies requires that effort be fixed in order to implement it. If effort is left unrestricted (MSO policies), a 127-mm mesh size will produce the greatest gross revenues and yield in weight and selection of an alternative mesh size would have a serious impact on fishery output (Table 5). Yield obtained from a 127-mm mesh is also least sensitive to the level of fishing effort, and will provide a profit over the widest range of effort levels.

Other Management Policy Consequences

There are trade-offs inherent in the choice of one management policy over another. For example, the MSY policy will produce the greatest aggregate yield, but only at the expense of efficiency. Similarly, gains in efficiency come only by sacrificing a portion of the potential yield. Also to be considered are the consequences of each management policy on species composition of the marketable yield. As indicated by their unit values (Table 1), English and particularly petrale sole appear to be more desirable than Dover sole. While both MSOY and MSY policies produce high aggregate yields, the production of petrale sole would actually be less than that which could be obtained with an efficiency-oriented strategy (Fig. 2). Similarly, although a 114-mm mesh is optimal for both efficiency-oriented strategies, a 127-mm mesh size would yield a somewhat more desirable species mix with only a slight reduction in yield and net revenues (Fig. 2).

Mesh size and effort regulations also influence the percent of the catch that will be marketable (retention rate). For a given mesh size, as effort increases, a greater portion of each year-class is harvested at a younger age, and hence, the average size of individuals in the catch decreases. For a fixed level of effort, undersized fish will also represent a greater share of the catch as mesh size decreases.

To maximize retention rate would require that no fishing effort occur, which is clearly not a feasible management option. On the other hand, retention rates should not be completely ignored. Low retention rates are associated with greater catch processing times and also indicate that a relatively large amount of unnecessary mortality has occurred. If when spawning stock abundance is low, recruitment is reduced, then high discard rates could contribute to serious stock declines. As expected, in this example, retention rates increase as mesh size increases, although, over a large range of effort levels, there is little advantage of using a 140-mm mesh over a 127-mm mesh (Fig. 3).

It should also be noted that regardless of which of these policies is considered, the aggregate yield is substantially less than that which would be obtained if each species could be

TABLE 5. Fishery yields for PMFC Area 2B that would result from the implementation of various management policies for various mesh sizes. Simulation results are from the mixed-species yield-per-recruit model described in the text. mt = metric tons.

Management policy	Yield characteristic	Mesh size (mm) 102	114	127	140
Maximization policies					
MSY	Marketable weight (mt)	1745.0	1941.9	2092.6	1528.7
MGR	Gross revenues (thousand dollars)	1359.3	1416.0	1437.3	1184.3
Efficiency-oriented policies					
MNR	Net revenues (thousand dollars)	1175.6	1209.4	1179.0	944.9
$f_{0.1}$	Marketable weight (mt)	1668.4	1812.7	1755.1	1020.8
Mesh size only policies					
MSOY	Marketable weight (mt) at zero net revenues	1235.8	1648.5	2092.2	1275.0
MSOGR	Gross revenues (thousand dollars) at zero net revenues	779.7	996.3	1265.4	1023.7

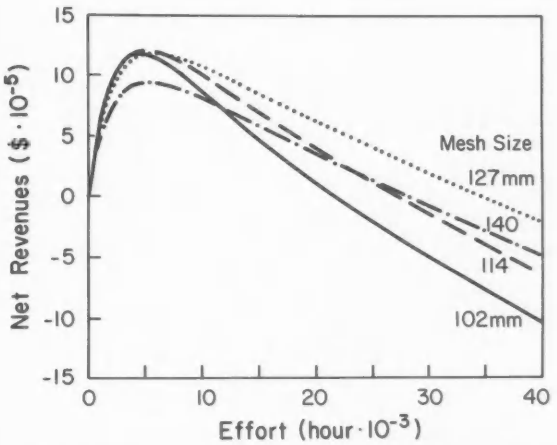

FIG. 1. Total net revenues generated by the Oregon flatfish fishery in PMFC Area 2B as a function of fishing effort and mesh size. Simulation results were obtained using the mixed-species yield-per-recruit model described in the text.

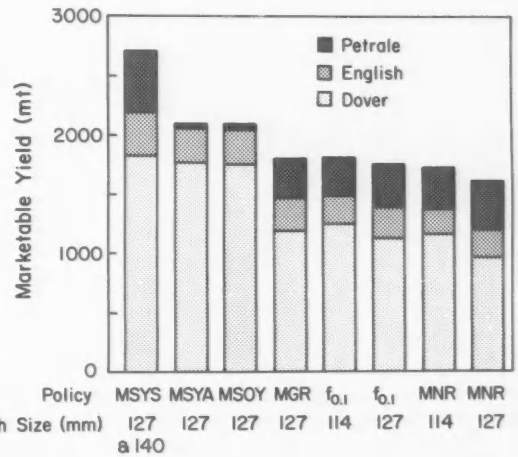

FIG. 2. Species composition of the marketable yield that would result from the implementation of various management policies. MSYS = sum of the single-species maximum sustained yields (MSY's); MSYA = MSY for the three-species aggregate; MSOY = mesh size only policy, maximum yield; MGR = maximum gross revenues policy; $f_{0.1}$ = $f_{0.1}$ policy (see text); MNR = maximum net revenues policy. Simulation results were obtained using the mixed-species yield-per-recruit model described in the text.

managed separately (Fig. 2). To maximize yields of Dover sole would require use of a 127-mm mesh, while a 140-mm mesh would be needed to obtain maximum yields of English and petrale soles. Maximization of individual species yields would also require that by-catch be eliminated and effort apportioned on a species-specific basis, which are currently not feasible management options.

Sensitivity of Results to Cost Estimates

Because the estimate of operating costs is only a rough approximation of actual costs, and because costs vary with interest rates, insurance rates, size composition of vessels in the fleet, and other factors, the sensitivity of the results to the assumed average cost per fishing hour was examined. Clearly, at a given effort level if costs are higher than estimated, profits will be lower than estimated, and vice versa. However, the mesh size that would allow the greatest profit to be made may or may not be sensitive to costs.

The only policies that require cost information are the MNR and MSO policies. To examine the sensitivity of optimal mesh size for these policies, yield isopleth diagrams were constructed using cost and mesh size as the independent variables and some characteristic of fishery output as the dependent variable. Costs were varied from zero to twice the estimated value of $36.42 per trawling hour.

For the MNR policy at the current estimate of costs the optimal mesh size is 114 mm, but both 127- and 102-mm mesh sizes produce similar levels of MNR (Fig. 4). As costs increase

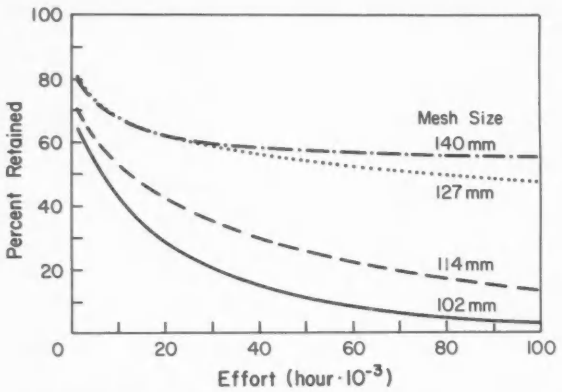

FIG. 3. Combined retention rates for three species of flatfish as a function of fishing effort and mesh size. Retention rate is the percent of the total weight caught that is marketable. Simulation results were obtained using the mixed-species yield-per-recruit model described in the text.

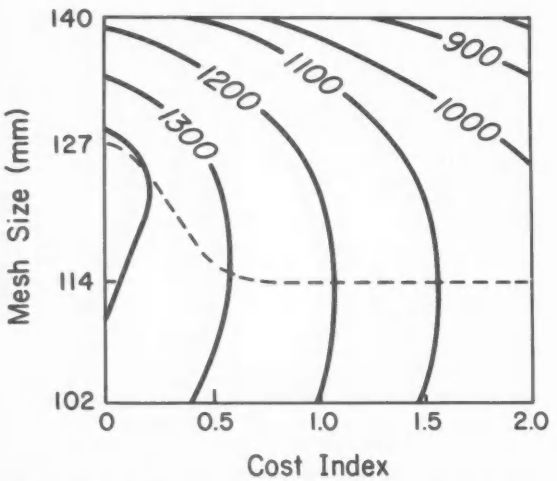

FIG. 4. Maximum net revenues (in thousand dollars; solid curves) as a function of operating costs and effort. For the operating cost index, a value of 1.0 represents the current estimate of operating costs ($36.42 per trawling hour), a value of 2.0 represents twice the estimated costs (i.e. $72.84 per hour), and so on. The optimal mesh curve represents the mesh size that yields the greatest maximum net revenues for each level of cost and is indicated by the broken curve. Simulation results were obtained using the mixed-species yield-per-recruit model described in the text.

the 114-mm mesh continues to produce highest levels of MNR, and the advantage of using a 114-mm mesh compared with other mesh sizes increases. As costs decrease, the 114-mm mesh remains optimal until costs reach low levels, at which point there is a slight advantage of shifting to a larger mesh size.

Yield isopleth diagrams were also constructed for the MSO policies using gross revenues, marketable weight, and effort at the point of zero net revenues as the dependent variables. Optimal mesh size remained at 127 mm for all three dependent variables over the range of costs considered, and thus yield isopleth diagrams are not shown. However, in all three cases, the advantage of the 127-mm mesh size over the other mesh sizes increases as costs increase.

The insensitivity of optimal mesh size to costs indicates that the simplifying assumptions made regarding costs (i.e. lack of discrimination between fixed and variable costs, linear relationship between effort and costs) were adequate for the purposes of these analyses.

Sensitivity to Variations in Recruitment

In the foregoing analyses it was assumed that the number of recruits is constant, but differs for each species. In actuality, relative recruitment strength will vary among species over time, and moreover, the average level of recruitment will vary among areas. To examine sensitivity of optimal mesh size to variations in recruitment strength, several additional model runs were performed. In each run, recruitment of two of the species was held constant, while recruitment of the third species was varied from zero to four times the estimated value. For each management policy and species for which recruitment was varied, an optimal mesh size curve was derived (Fig. 5).

For the maximization policies, optimal mesh size is nearly insensitive to variations in recruitment. In particular, for the MSY policy, the optimal mesh size remains at 127 mm until Dover sole recruitment decreases to one-tenth or less of the estimated 1971–74 level. Optimal mesh size for the MGR policy is somewhat more sensitive to variations in recruitment. As for the MSY policy, low levels of Dover sole recruitment imply that a larger mesh size (140 mm) would be optimal. In addition, at high levels of petrale sole recruitment, optimal mesh size again increases to 140 mm, whereas very low levels of English sole recruitment lead to a decrease in optimal mesh size.

Optimal mesh size for the efficiency-oriented strategies is most sensitive to variations in recruitment. For the MNR policy, a relatively small increase in petrale sole recruitment would result in an increase in optimal mesh size, as would a small decrease in Dover sole recruitment. This high sensitivity of optimal mesh size to recruitment fluctuations indicates that to achieve the most efficient harvest of the flatfish resource under an MNR policy would require periodic adjustments in mesh size regulations. However, the performance of a constant, 114-mm mesh size is quite good, even at extreme levels of recruitment (Fig. 6). In addition, a 127-mm mesh would perform nearly as well (Fig. 7).

Overall, decreases in Dover sole recruitment lead to an increase in optimal mesh size, whereas increases have little or no effect. The reverse trend is seen in response to variations in petrale sole recruitment. Optimal mesh size is least sensitive to English sole recruitment strength, although very high levels result in a slight increase, and very low levels can produce a slight decrease in optimal mesh size.

Discussion

The current minimum mesh size restriction of 114 mm would be optimal for Area 2B under an efficiency-oriented policy. However, if management of flatfish continues to approximate an MSY policy, substantial gains in aggregate yield could be achieved by increasing minimum mesh size to 127 mm. If the management regime were to shift towards a more efficiency-oriented policy, a 127-mm mesh size would still perform relatively well compared with the optimal mesh. There are addi-

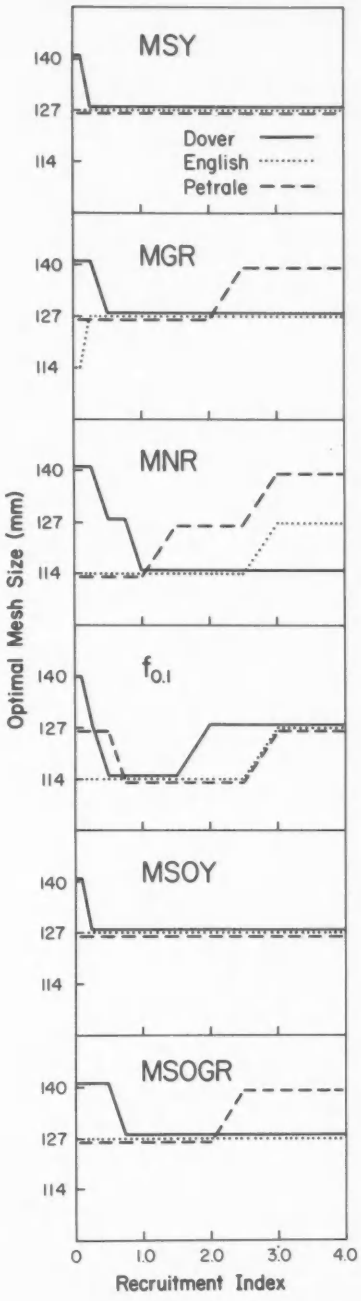

FIG. 5. Changes in optimal mesh size as a function of variations in recruitment of one species when that of the others is held constant, for various management policies. Information for all three species is shown on each graph. For the recruitment index, a value of 1.0 represents the current estimate of recruitment for PMFC Area 2B (see Table 1), 2.0 represents twice the current estimate, and so on. See text for explanation of management policy abbreviations. Simulation results were obtained using the mixed-species yield-per-recruit model described in the text.

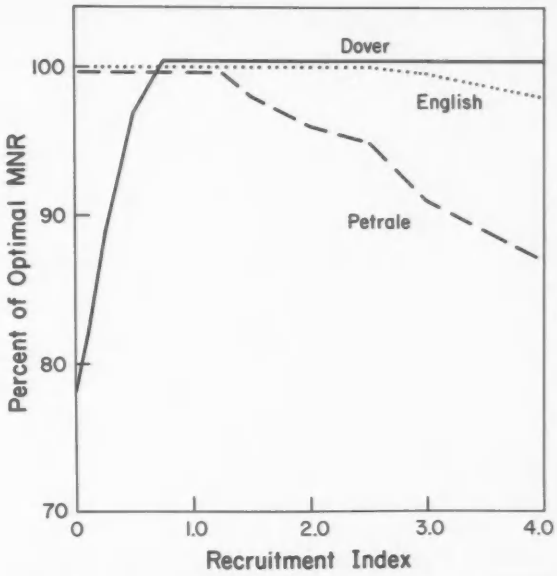

FIG. 6. Percent of optimal maximum net revenues (MNR) that would be generated in PMFC Area 2B using a constant mesh size of 114 mm but with variable recruitment of Dover, English, and petrale sole. Optimal MNR is defined as the greatest of the maximum net revenues generated by the four mesh sizes under consideration. For definition of the recruitment index, see caption to Fig. 5. Simulation results were obtained using the mixed-species yield-per-recruit model described in the text.

tional advantages to increasing mesh size to 127 mm. Because discard rates would be lower, time required to process the catch at sea would be reduced. Moreover, to the extent that spawning stock abundance has an effect on recruitment, a 127-mm mesh size is also a more biologically conservative choice. Finally, the species composition of the marketable yield that could be obtained with a 127-mm mesh size is generally more desirable than that obtainable with a 114-mm mesh size.

Although the sensitivity of optimal mesh size to relative recruitment levels differs for each management policy, increases in the relative abundance of petrale sole and decreases in the relative abundance of Dover sole tend to result in an increase in optimal mesh size. The relative abundance of Dover sole tends to be higher and that of petrale sole relatively lower in Area 2B than in other areas of the Oregon coast. Thus, it is likely that optimal mesh sizes for other areas would be somewhat higher than those applicable to Area 2B.

The following generalizations can be made concerning management policies of this three-species fishery. Optimal mesh size is more sensitive to the management policy selected than it is to variations in relative recruitment or to costs. Efficiency-oriented policies generally require a smaller mesh size to obtain optimal results than do MSO or maximization policies. Further, if economics become more important in formulating management policy, greater gains could be achieved by limiting effort than by altering mesh size regulations. However, as the management policy becomes less restrictive of effort, the influence of mesh size on fishery output increases.

Although only a limited number of policies were considered in these analyses, they likely represent the extremes that would

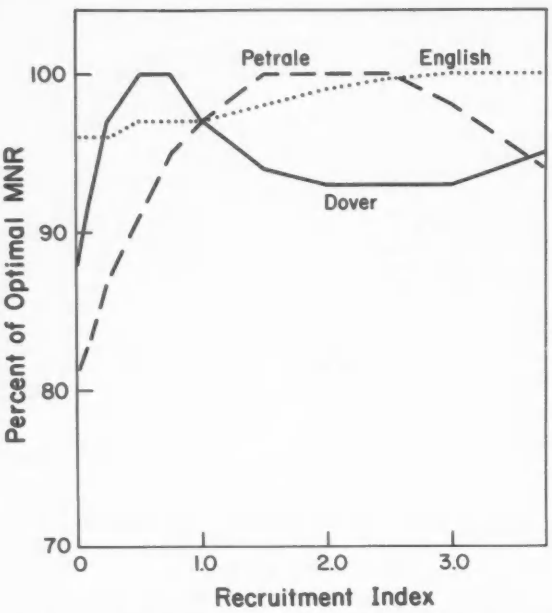

FIG. 7. Percent of optimal maximum net revenues (MNR) that would be generated in PMFC Area 2B using a constant mesh size of 127 mm, but with variable recruitment of Dover, English, and petrale sole. Optimal MNR is defined as the greatest of the maximum net revenues generated by the four mesh sizes under consideration. For definition of the recruitment index, see caption to Fig. 5. Simulation results were obtained using the mixed-species yield-per-recruit model described in the text.

be considered under most circumstances. That is, it is unlikely that a management strategy would be adopted which would require effort to be restricted below the level that produces MNR. At the other extreme, the maximum level of effort that need be considered will either be that coinciding with an MSOY or MSY policy, depending on the relationships of output and costs to effort and the nature of the management goal. It would generally be unwise to force effort above a level at which no net revenues are generated by the fishery. An exception to this would be in circumstances where meeting human food needs was the most important consideration, in which case, over the long run, an MSY policy is the best.

There is not a universally appropriate definition of optimal yield (Beverton and Holt 1957; Larkin 1977), and as a consequence, there is not a universally appropriate management policy. However, it would seem that under most definitions of optimal yield, the management policy that would be appropriate would fall within the range of management policies considered above.

A number of simplifying assumptions were made in constructing the analytical model, but the results were found to be relatively robust to violations of two key assumptions: constant recruitment and constant operating costs. It was also assumed that the relative unit values of the species and the relationship between the value of landings and the costs of fishing are constant. Further, the model does not discriminate between fixed and variable costs associated with fishing, and costs were expressed simply as a linear function of effort. To fully evaluate these assumptions, additional data must be collected over a number of years. If trends over time are found, they should be accounted for in future modeling work. However, the lack of sensitivity of results to varitions in costs indicates that the simplifying assumptions made regarding the economics components of the model were probably adequate.

Another assumption of the model that warrants further discussion is that species-specific catchability coefficients remain constant. Proportional changes in catchability coefficients (i.e. changes that do not affect the relative magnitudes of the coefficients among the three species) would reduce the levels of effort at which maximum yields, gross revenues, etc., are obtained for each mesh size, but should not have an impact on the relative yields among mesh sizes. Thus, results regarding optimal mesh sizes should be robust to proportional changes in catchability coefficients, which could occur, for example, due to advances in fishing technology over time.

Shifts in the relative magnitudes of the catchability coefficients of the three species could have a greater influence on the applicability of the results. As one species becomes less abundant, effort may shift away from areas where that species predominates and towards areas where the more abundant species are concentrated. Such shifts in effort would consequently impact catchability coefficients. On the other hand, according to the principle of supply and demand, as a species becomes less abundant, its relative price increases. This would tend to increase the amount of effort expended towards that species. Thus, depending on the sensitivity of price to supply, a decrease in the availability of a given species could result in either an increase or decrease in its catchability coefficient. The threefold difference in value among species, coupled with the moderating influence of availability on price, would suggest that shifts in catchability coefficients due to fluctuations in relative abundance would tend to be small.

Area management would be difficult and costly to enforce and would severely limit the freedom of fishermen. However, by controlling the amount of fishing effort by depth and area, it would be possible to directly alter species-specific catchability coefficients. Allocation of effort among areas on a finer scale would allow a closer approximation to single-species management. Because the sum of individual species MSY's always exceeds the MSY of the aggregate, area management would allow fishery yields to increase and the fishery could support a greater level of effort. These conclusions support the tenet postulated by Francis (1985) that "the more general or diverse the target of management is, the more biologically conservative the management policy must be in order to maintain long-term production of the resource base."

Acknowledgements

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Multispecies versus Single-Species Assessment of North Sea Fish Stocks

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Development of multispecies virtual population analysis (MSVPA), which assesses interspecific and intraspecific predation through an analysis of stomach contents, has verified the hypothesis that predation among exploited fish species contributes significantly to their natural mortality and that predation. and thus natural mortality, is inherently variable from year to year. In single-species virtual population analysis (SSVPA), natural mortality is assumed to be constant. MSVPA also suggests that natural mortality among young fish after recruitment is much higher than previously thought. Although catch quotas based on predictions of short-term catches from multispecies assessments would appear to differ little from those derived from single-species assessments, and certain problems remain to be resolved before multispecies assessments can be accepted for fish stock management, the method has considerable implications for management. For instance, it suggests that effects of mesh sizes and bycatch on fisheries need reevaluation and that year class strength may not be as fixed as previously assumed.

L'élaboration d'une analyse de population virtuelle multispécifique (APVM), qui permet d'évaluer la prédation inter et intraspécifique par analyse des contenus stomacaux, a permis de confirmer l'hypothèse voulant que la prédation au sein des espèces de poissons exploitées contribue de façon appréciable à leur mortalité naturelle et que la prédation, et par conséquent la mortalité naturelle, varie essentiellement d'une année à l'autre. En analyse de population virtuelle monospécifique, la mortalité naturelle est supposée constante. L'approche par APVM porte aussi à croire que la mortalité naturelle des jeunes poissons après le recrutement soit beaucoup plus élevée que l'on ne l'avait antérieurement supposée. Les contingents de prises basés sur des prévisions de captures à court terme obtenues par évaluation de plusieurs espèces diffèreraient très peu de ceux reposant sur des évaluations par espèces uniques et certains problèmes devront être résolus avant que les évaluations multispécifiques puissent être utilisées en gestion des stocks. Cette méthode présente cependant un grand intérêt. Ainsi, elle indique que les effets sur les pêches des tailles de mailles et des prises occasionnelles devraient être réévalués et que l'importance des classes annuelles pourrait ne pas être aussi constante que l'on ne l'avait supposée.

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After a long tradition of single-species assessment as the main basis of fish stock management, fishery science has moved into a new era where multispecies approaches receive due attention (Mercer 1982). The concept of multispecies assessment recognizes that fish species do not exist independently of each other and also that they are not harvested independently. The effects of these two types of interaction are different. On the one hand, biological interactions may modify the expected response of a particular stock to a management policy aimed at optimization of the yield by regulating the specific fishery on that stock. On the other hand, technological interactions between fisheries will rather tend to invalidate management measures introduced under such a policy.

In the North Sea a large number of countries, each characterized by a variety of fleets, are heavily exploiting the total fish community and technological interactions are consequently very complex. However, within the International Council for the Exploration of the Sea (ICES), research priorities have been focussed on the evaluation of predator–prey interactions in the area (Anonymous 1980) because the major changes in the fish community observed in the late 1960's and early 1970's (Andersen and Ursin 1977; Hempel 1978; Daan 1980) signify the likely impact of biological interactions on the yields of individual species. As Sparre (1979) and Ursin (1982) have pointed out, the single-species yield per recruit approach leads to severe inconsistencies when applied to predator and prey stocks simultaneously.

Species interactions may affect fish population dynamics in several ways. The more obvious one is that one species feeds upon another. Predation may occur in the prerecruit phase, in which case recruitment to the exploitable prey stock will be affected, or in the postrecruit phase, leading to direct competition between predator and fishery. Between two stocks, interactions may operate in different directions and food web structure may be accordingly complex. For instance, herring larvae contribute to the food of juvenile cod and juvenile herring to the food of adult cod, but cod eggs have been found in herring stomachs as well, and cannibalism has been reported for both species (Daan 1973; Daan et al. 1985). In addition, biological interactions could also evolve through competition for a common food resource. However, as concluded by Sissenwine (1984) in a comprehensive review of competition and predation in relation to recruitment, recent evidence points to predation as the predominant factor.

Among the great many interactions between various components of the ecosystem that can be envisaged, direct interactions between exploited fish species, either in the prerecruit or in the postrecruit phase, require special attention. From a management point of view, these are the more interesting because their effects could be taken into account in active management planning. Since "pest control" in large marine areas is not feasible unless the pest itself has some economic value, interactions with unexploited predators or prey, which may come and go uncontrolled, are of less interest.

Although in the long term, interactions in the early egg and larval phase may be the more significant ones, particularly in determining levels of recruitment, the assessment models presently available are not capable of treating prerecruit life stages satisfactorily. To keep a close link with traditional assessment techniques, it appeared appropriate to first explore possibilities to obtain estimates of predation mortalities among exploited fish populations with a view to alleviating the stringent assumption of constant natural mortality, characteristic of single-species models.

Traditionally, estimation of natural mortality rates causes a major problem in fisheries research, and the reliability of the values used in routine stock assessment is often questionable. However, the description of interspecific predation processes developed by Andersen and Ursin (1977) in their North Sea ecosystem model proved a useful starting point for inclusion in standard single-species virtual population analysis (SSVPA, Gulland 1965). In the simultaneous multispecies virtual population analysis (MSVPA, Pope 1979; Helgason and Gislason 1979), that part of the natural mortality caused by predation among the species included in the data set can be estimated, although the assumption of a constant "remaining natural mortality" at a predetermined rate is still unavoidable.

Essentially, the MSVPA requires reliable information on the annual food composition for the various predators by age group. Since available feeding studies rarely exhibited the required quality of data, a stomach sampling project was initiated in 1981 (Anonymous 1982, 1984a; Daan 1983). The results have been applied in trial runs with the MSVPA in 1984 (Anonymous 1984b).

This paper describes the multispecies assessments approach developed within ICES and discusses the major findings obtained to date in order to identify its potential value in general fish stock management.

The Predation Model

The MSVPA estimates simultaneously the number of each species at each age in the sea, the fishery mortalities, and the predation mortalities. These estimates are based on sets of three equations which link the numbers of each prey cohort present in the sea with the numbers caught in the fisheries and the numbers consumed by all predators. The number of fish of each cohort surviving at the end of the year is related to the number present at the beginning of that year according to

$$(1) \quad N_{i+1} = N_i \cdot \mathrm{EXP}(-(F_i + P_i + M))$$

where F represents the fishery mortality coefficient, P the predation mortality coefficient due to all predator cohorts included in the data set, and M the constant remaining mortality coefficient representing all other causes of natural deaths. The subscript i identifies the age of a cohort.

The total commercial catch in numbers (C) is related to the decrease in numbers of the cohort by

$$(2) \quad C_i = (F_i/(F_i + P_i + M)) \cdot (N_i - N_{i+1}).$$

These two equations represent the well–established basis for the SSVPA (Gulland 1965), with the exception that the natural mortality is split into two components. Using the subscript i now for a prey cohort and j for a predator cohort, the predation mortality is equal to the rate of food intake by all predators times the fraction of the total food that consists of i, divided by the biomass of i:

$$(3) \quad P_i = (1/(N_i \cdot w_i)) \sum_j (dI_j/dt) \cdot N_j \cdot (\mathrm{PHI}_{ij}/\mathrm{PHI}_j)$$

where dI/dt represents the rate of food intake, $\mathrm{PHI}(ij)/\mathrm{PHI}(j)$ the fraction of the total food of predator j that consists of prey i, and w the average weight of an individual prey in the sea.

By means of this straightforward description, the MSVPA equations can be solved without having to make any more assumptions than required for solving the individual SSVPA's, if estimates of food intake and also of the fraction of the total food of each predator cohort that consists of each prey cohort in each year are available.

Information on both food intake and food composition can be derived from stomach content data, but the condition that the data must be representative of the total annual population of each predator makes very high demands on the spatial and temporal collection of large numbers of samples. Although there appeared to be no option other than to sample at least one year satisfactorily, such an intensive program could not possibly be repeated on an annual basis, and for practical reasons, additional assumptions have been introduced which allow extrapolation from one reference year to other years.

The first assumption is that the rate of food intake is constant from year to year. This is supported by relatively small variation in average annual stomach content weight over large areas, (Daan 1983). A second assumption could be that the fractions of each prey in the total food of each predator remain constant. However, this simplification would seem unacceptable because the aim is to estimate variations in predation mortality, and the fractions must depend on changes in relative abundance of the prey. Therefore, Andersen and Ursin (1977) developed in their ecosystem model a preference function, which in a simplified version has been introduced in the MSVPA. The essence is that the fraction of each prey in the total food is a function of the abundance of that particular prey and all other possible prey weighted by a prey specific vulnerability index (v):

$$(4a) \quad \mathrm{PHI}_{ij} = v_{ij} \cdot N_i \cdot w_i \qquad [(0 \leq v_{ij} \leq 1)$$

and

$$(4b) \quad \mathrm{PHI}_j = \sum_i v_{ij} \cdot N_i \cdot W_i + v_{rj} \cdot B_r$$

where the index r indicates "other food" and B refers to biomass.

Obviously, the assumption that vulnerability does not change from year to year is less demanding because vulnerability can be viewed as a general concept reflecting, for instance, the size preference of a predator (Ursin 1973; Dekker 1983). Also, it may take account of ecological exclusion between predators and prey (Ursin 1982). A way to estimate the vulnerability matrix for all prey and predator age groups has been developed by Sparre (1984). The method is based on an additional loop in the MSVPA in which arbitrary starting values in the v matrix are

gradually adjusted so that ultimately the observed fractions in the year for which stomach content data are available correspond to the calculated fractions.

One remaining problem is related to the way other food is treated. Within the MSVPA, only numbers and weights of exploited fish species are considered, but a varying fraction of the food of different predators may consist of other species, which are put into the remainder term of (4b). Very little is known about the availability of other prey, and there is no other choice than to make a further assumption on how it changes from year to year. Pope (1979) simply assumed that "other food" constitutes a constant fraction of the food consumed. Helgason and Gislason (1979) assumed that the biomass of "other food" remains constant whereas Sparre (1980) proposed to keep the total available prey biomass constant, so that the expected changes in other prey would compensate for changes in exploited prey. In the absence of further evidence, the latter appears to be the more preferable because it is consistent with the assumption of a constant food intake whereas the others appear to imply a varying food intake.

Although critical additional assumptions have been introduced here, these could be tested later when reliable stomach content data become available for more than one year. Information on food composition in different years will allow tests of the goodness of fit of predicted versus observed fractions as well as evaluation of the variability in the vulnerability indices. Also, variation in the average amount of food in the stomach, which is an indication of the level of food intake, and the fraction "other food" can be used to verify the other hypotheses.

Stomach Sampling Project

Methods

On the basis of the theoretical framework summarized in the previous section, an internationally coordinated stomach sampling project was set up in 1981 which aimed at providing the required input data. There are 11 North Sea species which represent the bulk of the total annual fish yield and for which catch at age data are routinely collected. These are herring (*Clupea harengus*), sprat (*Sprattus sprattus*), cod (*Gadus morhua*), saithe (*Pollachius virens*), haddock (*Melanogrammus aeglefinus*), Norway pout (*Trisopterus esmarki*), whiting (*Merlangius merlangus*), sandeels (*Ammodytidae*), mackerel (*Scomber scomber*), plaice (*Pleuronectes platessa*), and sole (*Solea solea*). Of these, five principal fish predators were selected for stomach sampling: cod, whiting, saithe, mackerel, and haddock. To obtain information representative of the total annual populations, standardized trawl surveys were carried out in each quarter of 1981 over the entire North Sea, so that temporal and spatial variation in feeding and in distribution of the predators could be taken into account in the analysis. The stratum for collecting both stomach samples and information on catch rates, which were used as a weighting factor in raising the stomach content information over the area, was the ICES statistical rectangle defined by the grid in Fig. 1.

As a further requirement, the information collected had to be attributed to individual age classes, both in respect of predator and prey. Therefore, the stomach samples were grouped by predator size classes, and also the size of the exploited fish prey found in the stomachs was recorded so that at a later stage in the analysis the size distributions could be treated with age–size keys collected on the basis of area (cf, Fig. 1) during the surveys. Since the contribution of 0-group fish to predation mortalities in exploited age groups was expected to be insignificant, a minimum predator size limit of 10 cm was set for sampling stomachs. The grouped samples were analysed and both weights and numbers of prey by size class were recorded.

Nine countries participated in the sampling scheme, but to ensure complete homogeneity in processing of data within species, coordinators were made responsible for each of the five species and all samples collected were distributed accordingly for analysis.

On the basis of earlier experience in stomach sampling programs (Daan 1973), a quarterly target of 1500 stomachs by species was set as the minimum requirement for a reliable estimate of food composition.

In Table 1, a summary is given of the number of stomachs collected by species, quarter, and size class. A total of over 54 000 stomachs has been processed, and for three species the target was reached in all quarters. Regretfully, it turned out to be impossible to sample saithe and to a lesser extent mackerel at the required intensity because of low catch rates. As an example of the spatial coverage, the total numbers of cod stomachs sampled by statistical rectangle are indicated in Fig. 1.

Results

In the five species investigated, a high proportion of the stomach contents was found to represent exploited fish species. However, the prey species composition varied considerably not only in time and space but also with size, and thus age, of the predator (Table 2). Therefore, even within species it is difficult to make generalizations about food composition.

One observation that can be made from the differences between species is that they do reflect established differences in distribution and life habits of the predators. The bottom-dwelling cod and whiting inhabit the entire North Sea and have the most varied fish prey spectrum. They feed heavily on demersal roundfish, including their own relatives, although in whiting a relative shift to the pelagic clupeoids is apparent. Saithe has a semipelagic life style and its distribution is restricted to the deeper shelf waters of the northern North Sea. This species preys extremely heavily on Norway pout, which largely inhabits the same area and is also found regularly in midwater. Mackerel has almost exclusively pelagic prey. Haddock, which is widely distributed only in the northern part, depends largely on benthic food and is the least important fish predator. Significant numbers only of sandeels and Norway pout were found in haddock stomachs. Sandeels may occur close to the bottom but also in surface waters and they represent important prey for all predators at least during some stage of their life. Saithe were not found in stomachs, which reflects the inshore distribution of the younger age groups of this species. This distribution of young saithe is also clearly reflected in the complete absence of saithe smaller than 30 cm in the survey catches. Mackerel, plaice, and sole occur in low numbers in cod and whiting, but there is a strong indication from the size distributions that these prey are discarded fish from the commercial fishery (Daan 1973).

To calculate consumption rates, different stomach evacuation models have been used for the various species (Anonymous 1984a), but the estimated consumption rates appear to be on the low side when compared with requirements based on energetic considerations (Anonymous 1984b) and thus should be considered as underestimates. From the weights per prey and average

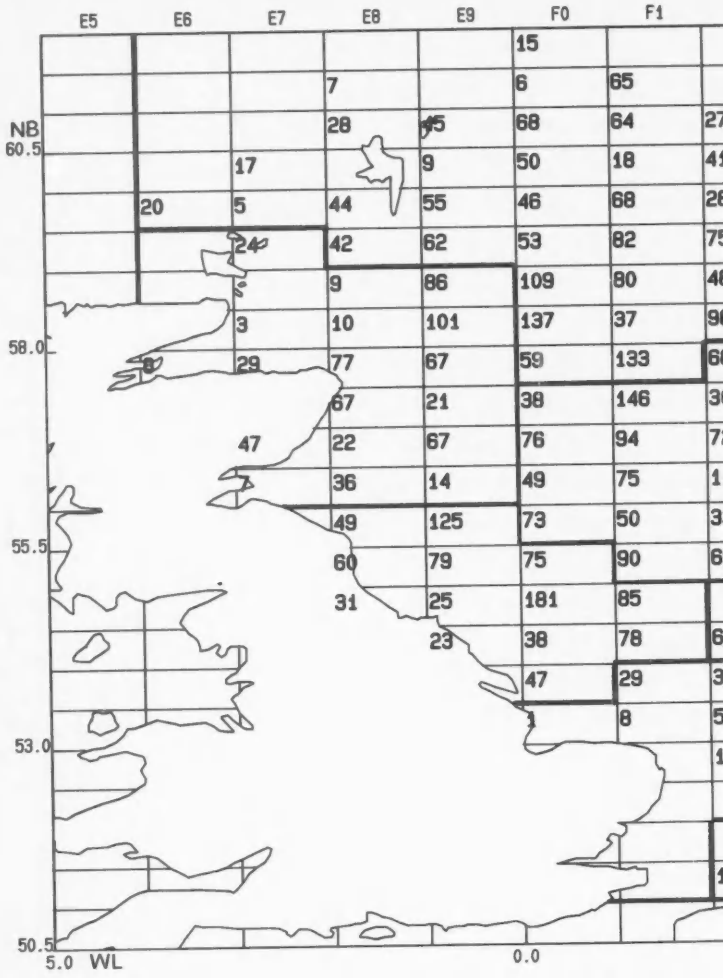
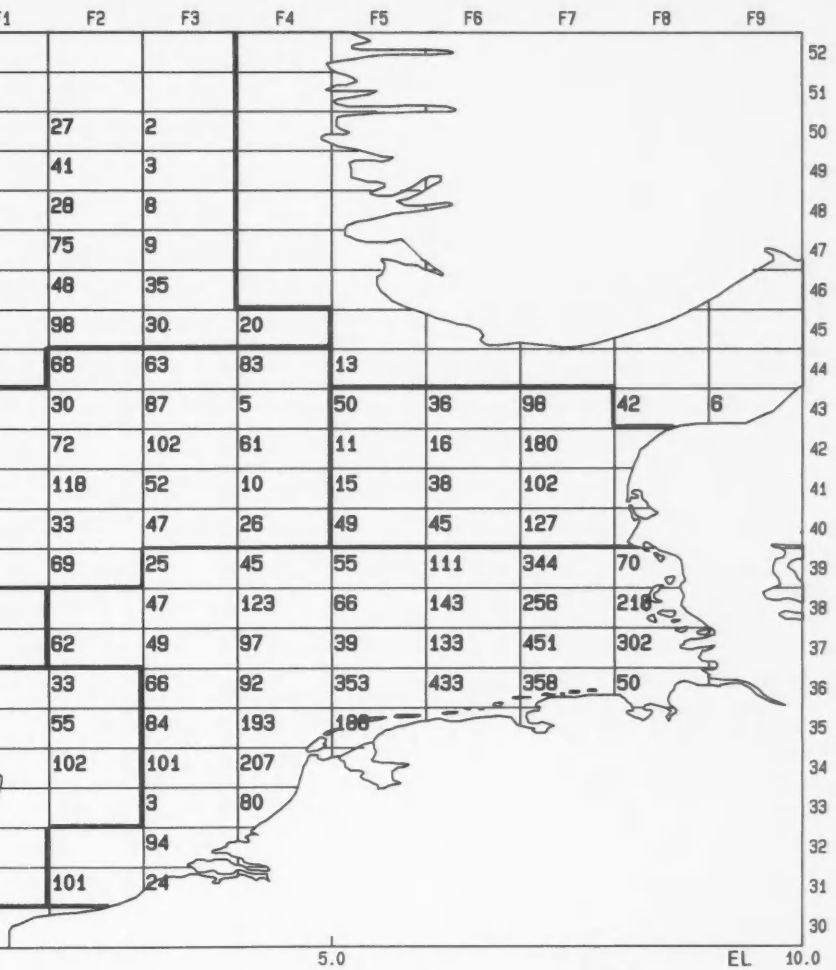


FIG. 1. Spatial distribution of the numbers of cod stomachs collected during 1981. The areas for collecting age–length keys is also indicated.



1. The grid identifies the sampling strata corresponding to ICES statistical rectangles, and the subdivision in

TABLE 1. Number of stomachs sampled in 1981 by species, quarter, and size group.

Species	Quarter				Size class (cm)										Total no. of stomachs
	1	2	3	4	7–10	0–15	15–20	20–25	25–30	30–40	40–50	50–70	70–100	≥100	
Cod	4180	2419	2345	2227	92	682	864	1147	1189	2148	1532	1656	1423	238	11 171
Whiting	7832	4211	3727	3447		2708	3234	4084	4729	3946	502	14			19 217
Saithe	336	185	428	379						59	170	413	487	199	1 328
Mackerel	246	1239	2737	693				{	1277	}	2576	1062			4 915
Haddock	2872	3726	5825	4966		2102	2508	3245	3721	4004	1523	280	6		16 389

prey weights the numbers of prey by species and age group consumed per year by predator age group can be estimated, and as an example, the cod data are reproduced in Table 3. Thus in 1981, each 2-yr-old cod was responsible for the deaths of 13 0-group cod and of 155 sandeels. Similar information is available for the other species (Anonymous 1984a). These results will not be dicussed in detail, but the general shift in age of prey with age of predator, indicative of the size preference, is evident.

The size preference of cod proved to be an outstanding feature in the stomach content data for cod, as shown by an elaborate study by Dekker (1983). He found a clear predator size – prey size relationship, which varied among different groups of prey but was relatively constant in time and space within fish. As an example, Fig. 2 provides the estimated log-normal preference function with standard deviation of fish eaten by cod in comparison with the observed mean prey length and associated standard deviations of fish in cod stomachs. It must be realized here that the observed prey sizes in the stomachs are a function not only of the size preference but also of the availability of prey of different sizes. A qualitative indication of the relative density of observations over the size range of prey and predator as well as of the estimated frequency distribution of the available fish prey in the sea is included in Fig. 2.

Size preference can be viewed as one of the factors contributing to the vulnerability of a particular prey to a particular predator (Ursin 1973). Since any prey cohort will cover a range of sizes, different predators may select different size classes. Thus, among 1-yr-old whiting, only the smaller ones may be eaten by 2-yr-old cod whereas older cod might select the larger individuals. This important aspect needs further investigation because in the model, the mean weight of individuals consumed is assumed to correspond to the mean weight in the sea for all predators whereas in reality, it is likely to vary considerably with predator.

Multispecies Virtual Population Analysis

Methods

In 1984 the results of the stomach sampling project were applied by the ad hoc Multispecies Assessment Working Group (Anonymous 1984b) in trial runs with the MSVPA program written by Sparre (1984). The group dealt with a large number of theoretical and practical problems related to MSVPA techniques, and I will restrict myself here to some general comments.

At the time of the meeting the haddock data were not yet available and therefore this predator had to be omited. Since consumption of plaice and sole was suspected to be related to discard rates in the commercial fishery, there was a danger of accounting twice for the same source of mortality; these species were therefore excluded from the analysis, which left the MSVPA to be run on only nine species. The data series covered 10 yr, starting from 1974. SSVPA's are traditionally run on an annual basis. Because the stomach content data were collected on a quarterly basis and since it was obvious that the presence of juvenile fish in the stomachs changed markedly from one quarter to another, reflecting the availability of juvenile fish of the right size to be eaten, it was decided to run the MSVPA on a quarterly basis too. However, this involved in some cases an arbitrary split of the annual catches over the quarters, and although the group intended not to deviate from SSVPA's in terms of terminal F-values, the change sometimes caused difficulties in tuning the quarterly input values to obtain annual values, which were similar to those obtained in the SSVPA's.

Another important problem was to decide upon the value of the natural mortality remaining from causes other than predation by exploited fish species. Again in order to minimize differences, the remaining natural mortality was taken as a constant equal to the total natural mortality in the SSVPA minus the estimated predation mortality on the oldest age groups in trial runs.

In equations (3) and (4) the same average prey weights by age group apply both to fish in the sea and to fish consumed. This formulation implies that mortality in terms of numbers equals mortality in terms of biomass. However, in a tentative analysis of the average prey weights in the stomachs, it was observed that indeed, as suggested by the pronounced size preference discussed in the former section, these are correlated with predator age. Since for most prey age groups, with an exception of 0-age fish, the average weight of prey items consumed is less than the average weight in the prey population, the formulation used presently in the MSVPA tends to underestimate predation mortalities. In future, adjustments are necessary.

The output of the MSVPA includes listings of stock sizes, fishery mortalities, predation mortalities, vulnerability matrices, and "who eats who" tables for all species, and one of the main difficulties is how to summarize this massive output. At this stage it is still uncertain how to best present a comprehensive overview of the results, and I will only highlight a few general results here, comparing in particular those obtained by MSVPA with results obtained by SSVPA.

Results

There is a general congruency in the estimated fishery mortalities of cod, haddock, and whiting (Fig. 3) which applies equally to the corresponding stock sizes of adult fish. This is not unexpected because the older age groups are not suffering much

TABLE 2. Average percentage weight of exploited fish species in predator stomachs by age group.

Predator	Prey	Predator age group 1	2	3	4	5	6+
Cod	Cod	2.57	1.43	2.81	5.99	6.67	3.91
	Haddock	4.06	5.92	8.99	12.57	13.78	17.76
	Whiting	3.47	4.35	8.95	12.78	13.62	14.64
	Norway pout	3.48	7.59	9.32	8.07	7.24	2.28
	Herring	1.76	3.03	4.50	5.78	5.50	1.71
	Sprat	3.08	3.66	1.93	1.20	1.19	1.43
	Sandeels	11.67	11.10	8.04	4.13	2.84	2.69
	Plaice	0.02	0.03	0.03	0.23	0.65	4.26
	Sole	0.06	0.11	0.08	0.16	0.20	0.38
	Mackerel	0.02	1.91	1.63	1.14	1.10	1.18
	Total	30.19	39.13	46.28	52.05	52.79	50.24
Whiting	Cod	0.06	0.12	0.21	0.16	0.16	0.15
	Haddock	2.36	6.33	8.16	10.48	11.50	16.23
	Whiting	1.59	1.80	2.73	4.06	5.59	8.09
	Norway pout	4.07	9.03	15.00	18.66	17.49	17.00
	Herring	1.46	8.62	9.88	9.31	8.62	6.47
	Sprat	9.43	13.43	13.81	12.48	11.20	8.09
	Sandeels	33.63	23.37	19.30	14.98	11.85	11.89
	Sole	0.02	0.01	0.01	0.01	0.01	+
	Mackerel	—	+	0.04	0.11	0.14	0.43
	Total	52.62	62.71	69.14	70.25	66.56	68.35
Saithe	Cod	0.25	0.23	0.10	0.15	0.18	0.10
	Haddock	20.57	18.55	10.38	7.25	7.08	6.58
	Whiting	—	0.02	0.08	0.10	0.35	1.13
	Norway pout	4.08	9.30	21.23	37.18	39.38	44.75
	Herring	—	—	—	0.05	0.55	3.00
	Sprat	0.15	0.95	1.84	0.13	0.05	0.10
	Sandeels	49.75	42.75	25.38	0.85	1.15	1.78
	Total	74.80	71.80	59.01	45.71	48.74	57.44
Haddock	Haddock	0.03	0.06	0.12	0.14	0.07	—
	Whiting	+	0.02	0.04	0.01	—	0.05
	Norway pout	1.51	6.06	13.74	20.89	23.98	15.25
	Herring	—	+	0.08	0.01	0.02	0.05
	Sprat	0.05	0.34	0.84	0.13	0.06	0.16
	Sandeels	4.53	10.72	8.79	9.84	8.73	9.76
	Total	6.12	17.20	23.61	31.02	32.86	25.27

Predator	Prey	Predator age group 1/2	3/7	8+
Mackerel	Cod	—	0.03	—
	Haddock	—	0.31	—
	Whiting	—	0.01	—
	Norway pout	8.46	11.19	14.48
	Herring	0.14	0.50	0.46
	Sprat	0.03	1.13	0.84
	Sandeels	34.77	20.31	3.83
	Total	43.40	33.48	19.61

predation, and therefore, the MSVPA behaves entirely as the SSVPA's. The 0 age group of these roundfish species suffers very high predation rates, but predation mortalities fall sharply with age up to 3 yr. Clearly the total natural mortality on the juveniles is very much higher than previously assumed in single-species assessment (Table 4). This has a marked effect on the number of 1-yr-old recruits estimated to be present in the sea (Table 5).

TABLE 3. Estimated numbers of prey by species and age consumed in 1981 per individual cod by age group.

Prey and age group		Predator age group 0	1	2	3	4	5	6+
Cod	0	0.01	4.90	13.05	3.05	2.18	3.37	0.63
	1		0.01	0.18	0.76	4.34	4.21	0.98
	2			0.00	0.12	1.30	1.98	1.72
	3				0.00	0.05	0.05	0.04
Haddock	0		1.19	12.36	15.51	133.10	17.81	8.17
	1		0.07	1.00	5.60	12.56	5.83	5.04
	2			0.05	1.80	7.33	5.72	9.04
	3			0.00	0.03	0.34	0.26	1.57
	4			0.00	0.00	0.01	0.00	0.12
	5				0.00	0.00	0.00	0.00
Whiting	0	0.02	5.07	9.43	2.11	1.25	0.88	0.88
	1		0.08	1.71	5.83	9.76	7.33	7.53
	2			0.23	1.94	7.80	7.62	15.84
	3			0.00	0.37	1.91	2.16	4.40
	4			0.00	0.11	0.37	0.28	0.41
	5			0.00	0.01	0.03	0.02	0.09
	6			0.00	0.00	0.01	0.00	0.04
Norway pout	0	0.15	1.13	19.92	32.15	138.85	25.19	25.43
	1		0.06	4.02	22.35	33.27	26.51	11.43
	2		0.00	0.85	7.07	7.54	4.64	2.87
	3			0.00	0.13	0.19	0.13	0.07
Herring	0		0.45	1.56	4.40	0.14	0.03	
	1		1.46	1.21	1.72	1.99	1.12	1.64
	2		0.00	0.08	0.56	0.85	0.68	1.44
	3			0.13	1.38	2.61	1.72	1.22
	4			0.00	0.01	0.00		
	5			0.00	0.02	0.00		
	6			0.00	0.05	1.84	0.17	0.06
Sprat	0		1.59	0.60	0.16	0.15	0.24	0.39
	1	0.00	7.60	5.26	2.15	2.82	1.95	5.07
	2		2.19	5.12	4.13	6.25	5.24	9.41
	3		0.02	0.46	0.57	0.74	0.63	0.78
	4		0.00	0.00	0.01	0.03	0.00	0.00
Sandeels	0	0.60	23.65	155.02	116.20	112.34	77.80	0.00
	1		4.89	45.22	34.43	65.83	50.54	0.00
	2		1.42	4.19	9.81	15.69	4.88	0.00
	3		0.13	0.60	2.36	5.47	1.33	0.00
	4		0.06	0.31	2.25	2.90	1.02	0.00
	5		0.00	0.10	0.74	1.22	0.28	0.00
	6		0.00	0.06	0.72	0.68	0.27	27.38

Fishing mortality on adult herring appears to be much higher than indicated by the SSVPA (Fig. 3), despite the fact that predation mortality is zero. This is probably related to the strong seasonal character of the herring fishery because it was impossible to tune the terminal F-values in the quarterly MSVPA to correspond to the annual SSVPA values.

Sprat and Norway pout together with sandeels are short-lived species, which are exploited for the fish meal industry. Their stocks are commonly assessed with much higher natural mortality values than the others (Table 4). These higher values appear in general to agree with the estimated predation mortalities. The patterns in both fishery and predation mortality

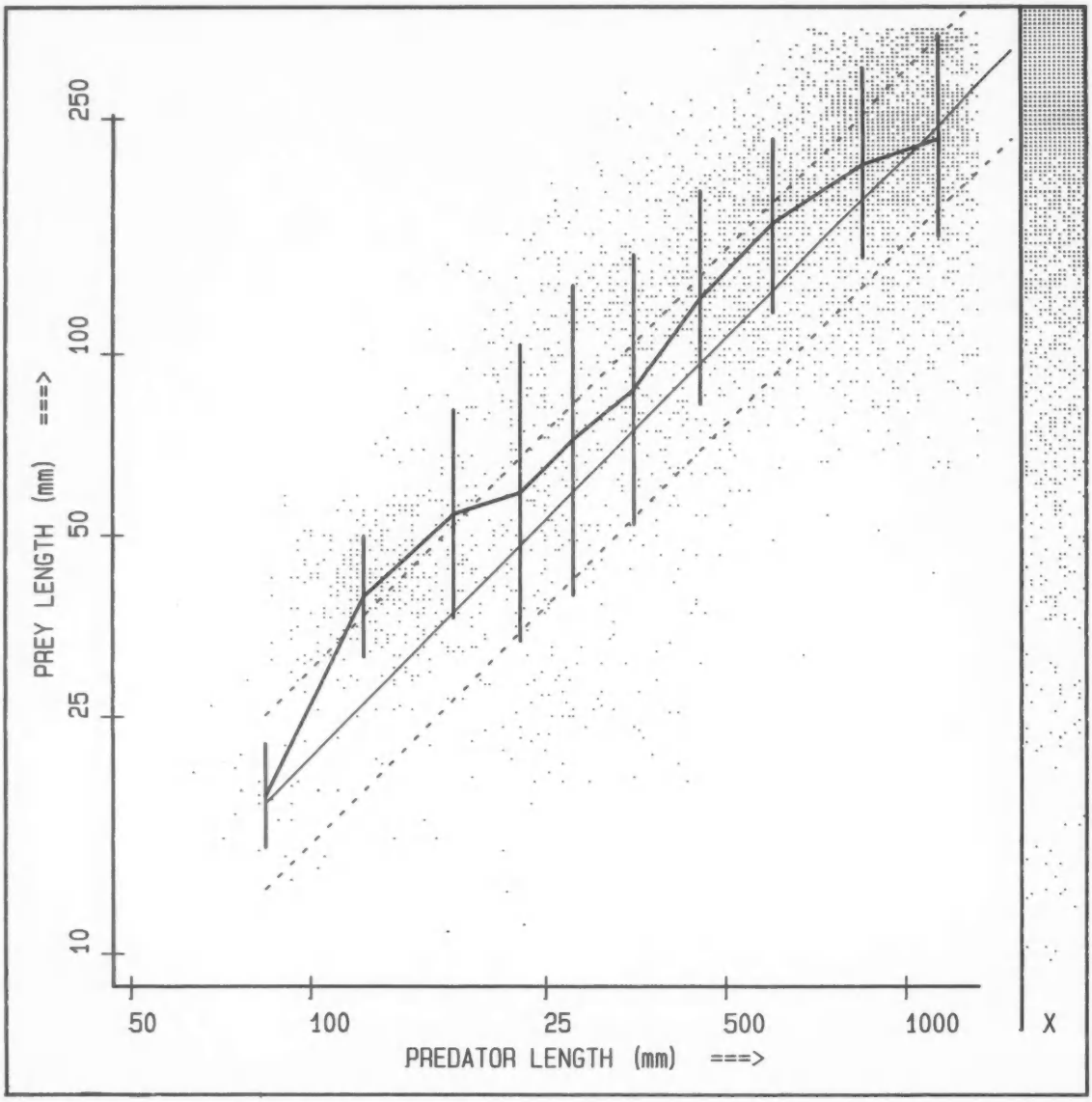


FIG. 2. Observed mean length of fish prey (heavy line) with associated standard deviations (vertical lines) in stomachs against predator length and the estimated preference function (thin line) with standard deviations (broken lines). The scattered points reflect relative density of observations, randomized within predator and prey classes. The *X*-column on the right represents the estimated frequency distribution of the available fish prey in the sea. (Redrawn from Dekker 1983)

with age are variable, which reflects the fact that VPA methods do not yield very reliable results for these species because the short life span inhibits stabilization of the estimated *F*-values around their true value.

If the assumptions that allow extrapolation from the 1981 stomach content data to other years are accepted, predation mortalities may easily vary by approximately 40% around the mean (Table 4). Regretfully, data from before the early 1970's, when the major changes in species composition of the North Sea fish community took place, are currently not available. It would seem likely that predation levels on demersal fish have increased due to the expansion of the demersal predators whereas predation on the short-lived species may have decreased due to the collapse of the stock of mackerel, one of their main predators.

Overall the fish predators consumed approximately the same fraction of the total exploitable fish biomass as the fishery took in two selected years (~20%, Table 6). However, since the predators exploit an entirely different part of the stocks, at least for the nonindustrial species, in terms of numbers the predators

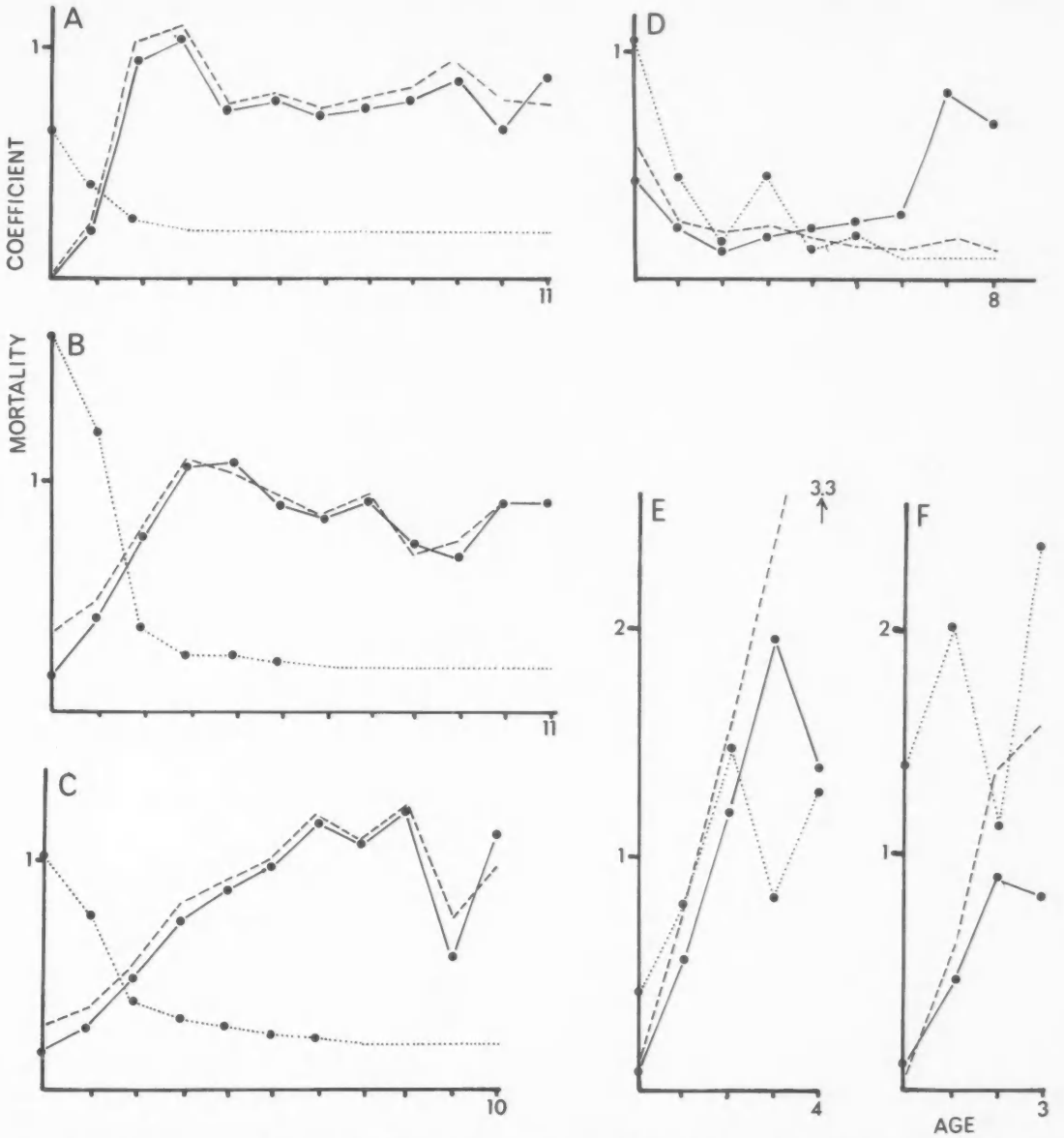


FIG. 3. Average fishery mortality coefficients (solid lines) and natural mortality coefficients (predation plus remaining mortality) (dotted lines) by age class estimated from MSVPA. For comparison, the average fishery mortality coefficients estimated from SSVPA are also indicated (broken lines). (A) Cod; (B) haddock; (C) whiting; (D) herring; (E) sprat; (F) Norway pout. (Redrawn from Anonymous 1984b)

remove many more though smaller fish. Total stock biomasses, predation, and commercial catches appear to have decreased simultaneously, but within species, trends are variable.

Discussion

One main conclusion from the trial runs with MSVPA so far is that for the adult fish the results agree well with traditional single-species assessments. Although not yet fully explored, it seems unlikely that MSVPA will affect the short-term catch predictions on which the advice on catch quota is based, when recent levels of exploitation are projected forward. This is because stock sizes and fishery mortalities change in proportion. However, the situation becomes rather different when the management strategy aims at changing short-term exploitation levels on particular stocks because of the variable impact of the predator stocks. In this case, also, the forward projection must be carried out in a multispecies fashion.

TABLE 4. Average predation mortality coefficients and range of estimated values for individual years in parentheses according to MSVPA in comparison with traditional natural mortality coefficient values in SSVPA.

		Cod	Haddock	Whiting	Norway pout	Herring	Sprat	Sandeel
MSVPA								
P	age 0	0.56 (0.4–0.6)	1.42 (1.2–1.8)	0.80 (0.8–1.1)	0.33 (0.3–0.9)	0.95 (0.8–1.2)	0.28 (0.2–0.6)	0.55 (0.4–1.0)
	1	0.33 (0.2–0.4)	1.04 (0.8–1.6)	0.65 (0.4–0.7)	0.96 (0.8–1.8)	0.38 (0.3–0.5)	0.62 (0.6–1.0)	0.65 (0.4–1.0)
	2	0.03 (0.02–0.05)	0.16 (0.15–0.3)	0.20 (0.2–0.3)	0.10 (0.08–0.2)	0.03 (0.02–0.04)	1.32 (1.1–2.0)	0.56 (0.4–0.8)
M	all	0.2	0.2	0.2	1.0	0.1	0.1	0.1
SSVPA								
M	all	0.2	0.2	0.2	1.6	0.1	0.8	0.5

TABLE 5. Average number of 1-yr-old fish (millions) in the sea (1974–83) estimated according to MSVPA and SSVPA.

Species	MSVPA	SSVPA	Fraction
Cod	299	230	1.30
Haddock	4 437	1 445	3.07
Whiting	3 142	1 650	1.90
Norway pout[a]	198 001	75 087	2.64
Herring	3 399	2 060	1.65
Sprat	192 750	81 500	2.37

[a]Average 1977–83.

More important, however, are the implications with regard to the selection of management objectives, which have until now been primarily based on some optimum yield per recruit concept. The yield per recruit appears to be not only a function of the level of exploitation on a particular stock, but it must also be viewed as a multidimensional plane, in which all stocks represent different axes. Because there is not just one optimum solution in a biological sense for exploiting the fish community, some common value must be given to the catches of different species. It would follow that within the multispecies approach, economic aspects cannot be avoided. This problem needs further attention, but for the time being it would seem reasonable to relate any biological management advice to stabilization of the fisheries at their present level, and not to propose dramatic reductions in fishing effort on the basis of unrealistic single-species yield per recruit concepts.

Scientifically, the exercise has been very rewarding. The planning of stomach sampling to meet the demands of a well-defined theoretical framework has undoubtly been a critical factor in allowing considerable progress to be made in estimating at least part of the natural mortality more accurately than has been possible before.

The high predation mortality on juvenile fish as estimated by MSVPA has important practical and theoretical implications. The age of first capture in the human consumption fisheries lies generally within the stage of life when predation mortality is still considerably higher than has been assumed formerly. Therefore, particularly for North Sea roundfish, past mesh assessments have undoubtedly overestimated long-term gains associated with increased mesh sizes. Similarly, the adverse effects of industrial fisheries on the human consumption stocks through the bycatch of juvenile fish have clearly been overemphasized. In classical procedures, estimation of natural mortality in juvenile fish has always raised a problem because log-abundance plots provide the combined effect of mortality and partial recruitment. Clearly, however, in the light of these new findings, mortalities of older fish should not be extrapolated to juvenile fish, and both types of assessment need reevaluation. The observed interactions also have a considerable bearing on general estimates of biological productivity of these fish stocks, a larger proportion of which must be attributed to juveniles. The variable predation pressure after the age when young fish have recruited to the exploitable biomass indicates that year class strength may not be as fixed as has been assumed before.

In principle, the equations underlying MSVPA can also be applied in a predictive mode for short-term catch projections. No efforts to do this have yet been made, but it is expected that under stable exploitation levels multispecies assessment will have only marginal effects on predicted catches as compared with single-species assessment (Anonymous 1984b). The reason is that larger stock sizes of juveniles in MSVPA are compensated by lower estimates of fishing mortality whereas the adult population is virtually the same in both cases.

Notwithstanding the positive results of applying MSVPA techniques, it must be realized that it does not represent a revolutionary new method of stock assessment. It rather is an extension of traditional methods aimed at quantitative estimation of a very specific type of interaction only. Because the choice of a particular value of the remaining natural mortality is still largely a matter of guesswork, the method does not result in reliable estimates of total natural mortality, but rather enables us to determine a lower limit. Interactions in the early life stages are also not accounted for, and therefore the MSVPA is unlikely to contribute significantly to the identification of the causal mechanisms behind the large fluctuations in year class strength from year to year. This remains an important problem in fisheries research. If the data series could be extended backwards to cover the 1960's, more insight would be obtained in the possible scale of changes in predator–prey interactions, but the reasons for the observed changes in the fish community would probably remain unresolved.

At this stage the multispecies approach has not replaced the single-species assessment as the basis for fish stock management in the ICES area. There are still too many uncertainties in the underlying assumptions of the model to be generally accepted. More importantly, however, it represents only a tool that assists in evaluating past changes, and as long as sound multispecies management objectives have not been formulated, the scope of this approach is bound to remain limited. Still, the results obtained so far do cast their shadow ahead on the work of the ICES single-species assessment working groups, and adjustments will be necessary. In the meantime, both on the theoretical and the practical side, work is in progress to improve

TABLE 6. Estimated stock biomasses and weights consumed ('000 tonnes) of North Sea fish stocks in 1974 and 1981 according to MSVPA in comparison with yields.

Prey	Stock biomass	Weights consumed by predator: Cod	Whiting	Saithe	Mackerel	Total	% consumed	Catch	% caught
				1974					
Cod	395	14	1	1	0	16	3.6	203	51.3
Whiting	862	88	43	3	0	135	15.6	290	33.6
Saithe	1 028	0	0	0	0	0	—	274	26.7
Mackerel	1 148	0	0	0	0	0	—	298	26.0
Haddock	2 240	189	154	341	28	713	31.8	364	16.3
Herring	487	22	21	6	5	53	10.9	275	56.5
Sprat	4 168	112	425	6	210	753	18.1	314	7.5
Norway pout	3 695	81	90	578	281	1 030	27.9	736	19.9
Sandeel	2 662	64	243	17	706	1 031	38.7	524	19.7
Total	16 686	570	978	952	1 230	3 730	22.4	3 278	19.6
				1981					
Cod	505	34	2	1	0	37	7.4	358	71.2
Whiting	571	87	35	2	0	124	21.7	192	33.6
Saithe	659	0	0	0	0	0	—	127	19.3
Mackerel	191	0	0	0	0	0	—	67	35.1
Haddock	613	90	86	46	0	222	36.0	208	33.9
Herring	651	41	114	7	2	164	25.2	141	21.7
Sprat	502	48	120	1	3	172	34.2	209	41.6
Norway pout	4 180	81	145	287	46	560	11.7	235	5.6
Sandeel	1 713	122	274	10	85	490	27.2	569	33.2
Total	9 587	504	776	353	137	1 770	18.5	2 106	22.0

the basis of MSVPA. A new stomach sampling program was initiated in 1985 to address specifically the assumption of constant vulnerability.

The MSVPA is typically applicable in areas where reliable, detailed catch statistics exist. Since on a worldwide scale such areas are limited in extent, the scope for application is similarly limited. Unfortunately, even in the eastern Atlantic, catch statistics are deteriorating rapidly as a direct consequence of the choice to try to manage fisheries by means of catch quotas before problems of enforcement have been solved. Falsification of reported landings appears to have become common practice among both fishermen and responsible agencies. Since total catch by age group is the essential input of VPA, the reliability of the assessments deteriorates proportionately. These problems affect single-species and multispecies assessments equally, but from a scientific point of view it is unfortunate that when progress is being made towards the solution of some major interaction problems, collection of data to evaluate these interactions is declining.

For several reasons it may not be possible to apply MSVPA methods elsewhere. However, the conclusion that natural mortalities are high and variable among juvenile fish communities where both predatory fish and prey stocks are heavily exploited may be more general than was previously thought. Due attention to such interactions would seem critical before appropriate management policies can be formulated.

Acknowledgements

The ICES stomach sampling project as well as the development of multispecies assessment has involved a large number of people at all stages between collection of material and ultimate application in sophisticated models. Although it is impossible to identify all participants individually, this report by no means represents a personal accomplishment, but is a reflection of a large-scale internationally coordinated research program which could only be conducted through the integrated effort of many scientists.

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Yield and Dynamics of Destabilized Chub (*Coregonus* spp.) Populations in Lakes Michigan and Huron, 1950–84[1]

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Brown, E. H. Jr., R. L. Argyle, N. R. Payne, and M. E. Holey. 1987. Yield and dynamics of destabilized chub (*Coregonus* spp.) populations in Lakes Michigan and Huron, 1950–84. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 371–383.

Deepwater ciscoes (*Coregonus* spp.) or "chubs" of Lake Michigan far surpassed those of Lake Huron in yield, population density, and resilience following severe depletion in the 1960s and 1970s, when the bloater (*C. hoyi*) composed more than 90% of the stocks. The population decline of bloaters in recent decades was mainly attributed to exploitation, to the depression of chub recruitment (e.g. from inferred predation on early life stages) by nonendemic alewives (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*), and to complications arising from extreme female predominance that was best documented for Lake Michigan. The various interactions between bloaters and the nonendemic species, which were intensified after the loss of large predators to sea lamprey (*Petromyzon marinus*), would help to explain why a stock–recruitment relation was not shown for the Lake Michigan bloater. We hypothesize that reproductive inefficiency caused by a shift to strong female predominance in the bloater depresses recruitment and thus helps to regulate abundance. However, the low resilience that sex imbalance seems to impart makes the stock unstable when exploited. It should therefore be exploited conservatively during such periods. Also, the sex ratio and its direction of change appear to be important qualifiers when surplus production is estimated from stock size.

Les ciscos de profondeur (*Coregonus* spp.) du lac Michigan sont de beaucoup supérieurs à ceux du lac Huron si l'on considère le rendement, la densité de population et la possibilité de se rétablir suite à la forte baisse de population des années 1960 et 1970, quand le cisco de fumage (*C. hoyi*) constituait plus de 90 % des stocks. Le déclin des populations de ciscos de fumage noté au cours des dernières décennies a en grande partie été attribué à l'exploitation, à la chute du recrutement des ciscos de profondeur (prédation supposée des premiers stades de développement) due au gaspareau non indigène (*Alosa pseudoharengus*) et à l'éperlan arc-en-ciel (*Osmerus mordax*), et à des complications résultant d'une prédominance extrême des femelles, comme au lac Michigan où ce phénomène a été le mieux décrit. Les diverses interactions entre les ciscos de fumage et les espèces non indigènes, qui se sont intensifiées après la disparition des gros prédateurs suite à la prédation par la lamproie marine (*Petromyzon marinus*), devraient permettre d'expliquer pourquoi on n'a pas noté de relation stock– recrutement pour le cisco de fumage du la Michigan. Les auteurs formulent l'hypothèse que l'inefficacité de la reproduction découlant d'une forte prédominance des femelles chez le cisco de fumage a nui au recrutement et donc favorisé la régulation de l'abondance. La faible capacité de rétablissement qui semble découler du déséquilibre des sexes rend cependant le stock instable lorsqu'il est exploité. Il devrait donc étre exploité de façon assez limitée au cours de ces périodes. De plus, le rapport des sexes et la direction de sa modification sont des paramètres importants de l'estimation de la production excédentaire faite à partir de la taille du stock.

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The deepwater ciscoes (*Coregonus* spp.) which are fished and marketed in the aggregate as "chubs," were important components of the cold-water fish communities that evolved in Lake Michigan, Lake Huron, and other Great Lakes after the last glacial period (Moffett 1957). Together with their close relative the lake herring (*Coregonus artedii*), they provided forage for predators (principally lake trout, *Salvelinus namaycush* and burbot, *Lota lota*) and, beginning in the 1800s, salted and smoked products for human consumption. These endemic fish communities, which were structurally simple in terms of species numbers and diversity, have been altered substantially and destabilized by processes that originated or accelerated in the mid-1900s. The greatest ecological impacts

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have been attributed to exploitation and to invading or introduced exotic species of marine origin, including in order of first occurrence rainbow smelt (*Osmerus mordax*), sea lamprey (*Petromyzon marinus*), and alewife (*Alosa pseudoharengus*).

Seven species of deepwater ciscoes were once recognized from the Great Lakes, but Michigan was the only lake to contain all seven (Koelz 1929; Smith 1964). The plastic morphometric and meristic characters of the different species made their taxonomic status questionable and their identification as juveniles difficult or impossible (Smith and Todd 1984). The bloater (*C. hoyi*), smallest of the seven species, is the only cisco that has persisted in significant harvestable quantities in Lakes Michigan and Huron since the 1950s. Hence the terms bloater and chub are now nearly synonymous in reference to the commercial fisheries in these lakes.

Destruction of lake trout and burbot by sea lampreys in Lakes Michigan and Huron in the 1940s and 1950s removed the primary source of predation on bloaters, and the depletion or extirpation of the larger species of ciscoes by selective fishing and lampreys (Smith 1968) reduced possible competitors. These changes enabled bloaters to become extremely abundant at first, but may also have hastened the invasion of each lake by alewives, which have adversely affected ciscoes and other native species (Smith 1970). Since the late 1970s, bloaters have been recovering vigorously from severe depletion in Lake Michigan and less so from total collapse in Lake Huron.

The objectives of this study were to compare yields to fisheries and dynamics of chub populations in Lake Michigan, Lake Huron proper, and Georgian Bay (Fig. 1), elucidating possible limiting factors and population regulating mechanisms that have affected yields. Special emphasis is placed on the dynamics of the bloater before and during its recent recoveries.

Data Base and Methods

This study is based on information provided by state, provincial, and federal resource agencies from the following data files: (1) commercial fishery statistics on chubs compiled from mandatory reporting by fishermen in the various jurisdictions and (2) catch–effort statistics and biological data (e.g. age, length, weight, sex, and maturity) on chubs and associated species (i.e. alewives and smelt) sampled mainly with bottom trawls and graded-mesh gill nets from agency boats and research vessels.

Small-mesh gill nets (mesh sizes of about 64–70 mm stretched measure) were the "standard" gear of the commercial fisheries for chubs throughout the study period, with one important exception: otter trawls were introduced to take small chubs for animal food in several regions of Lake Michigan in 1959 but were switched from chubs to the rapidly expanding alewife population as their primary target in the mid-1960s. We expressed the trawl effort and the nominal effort of miscellaneous gears as standard gillnet effort by dividing the catches with these gears by the catch-per-unit-effort (CPE) of small-mesh gill nets fished in the same periods.

To enable direct comparisons between lakes and between regions within lakes, we expressed commercial yields and fishing intensity as kilograms of chubs (in the round) and metres of gill net lifted, respectively, per hectare of fishable habitat. Fishable habitat in a commercial context was defined arbitrarily as waters 36–110 m deep, which contain most of the fishable biomass of chubs in Lakes Michigan and Huron (Brown et al. 1985; National Fisheries Center – Great Lakes, unpubl. data).

FIG. 1. Lake Michigan, Lake Huron proper, and Georgian Bay in relation to other Great Lakes and to state, provincial, and international boundaries.

We estimated the size of standing stocks of bloaters available to bottom trawls in Lake Michigan (fall 1967–84) and U.S. waters of Lake Huron (spring and fall 1973–84) to provide a more accurate and complete basis for examining stock dynamics than was possible with incomplete biological data from the periodically disrupted commercial fisheries. (The estimates for Lake Michigan were partitioned according to ages determined from scales and used in several age-related analyses.) The standing stock estimates are totals for each lake of the summations across depth strata, within geographic sectors sampled systematically at fixed index stations, of the stratum area times catch-per-unit-area (Hatch et al. 1981; Argyle 1982). We computed population density (kilograms per hectare) of bloaters and of alewives and smelt sampled in the same surveys, but used a wider depth range (0–110 m) than in the commercial yield analysis, to include productive inshore waters where younger fish were generally most abundant.

Yield Relative to Fishing Intensity, Stock Size, and Other Determinants

The yields of chubs at different levels of fishing intensity in Lakes Michigan and Huron since 1950 reflect real interlake differences in productivity, despite the complicating effects of major ecological changes on the fish communities. These yields are the best available indices of those that would be expected during various ecological states that have transpired in the lakes and which appear to be partly reevolving (Loftus et al. 1987; Eck and Wells 1987).

Lake Michigan chub populations were more productive and were fished much more intensively than those in U.S. and Canadian waters of Lake Huron during most of the post-1950 period (Fig. 2 and 3). Chub yield frequently exceeded 2 kg/ha in Lake Michigan through 1970, and then began an alarming decline that the states of Illinois, Michigan, and Wisconsin reacted to by obtaining a lakewide ban on chub fishing in 1976

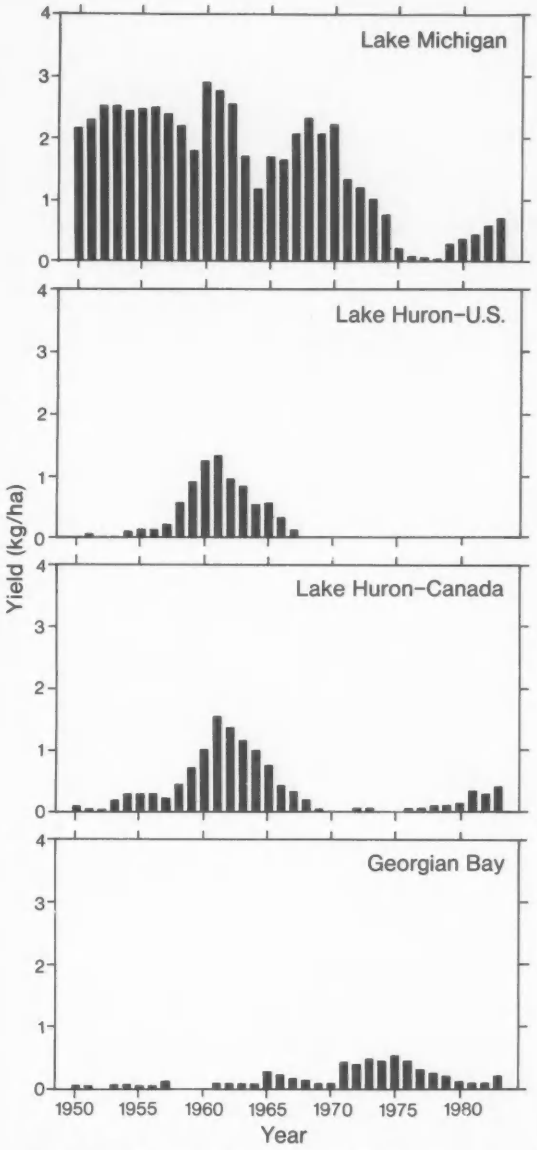

FIG. 2. Commercial yields of chubs in round weight per unit area of fishable habitat (water 37–110 m deep) in Lake Michigan, U.S. and Canadian waters of Lake Huron proper, and Georgian Bay, 1950–83.

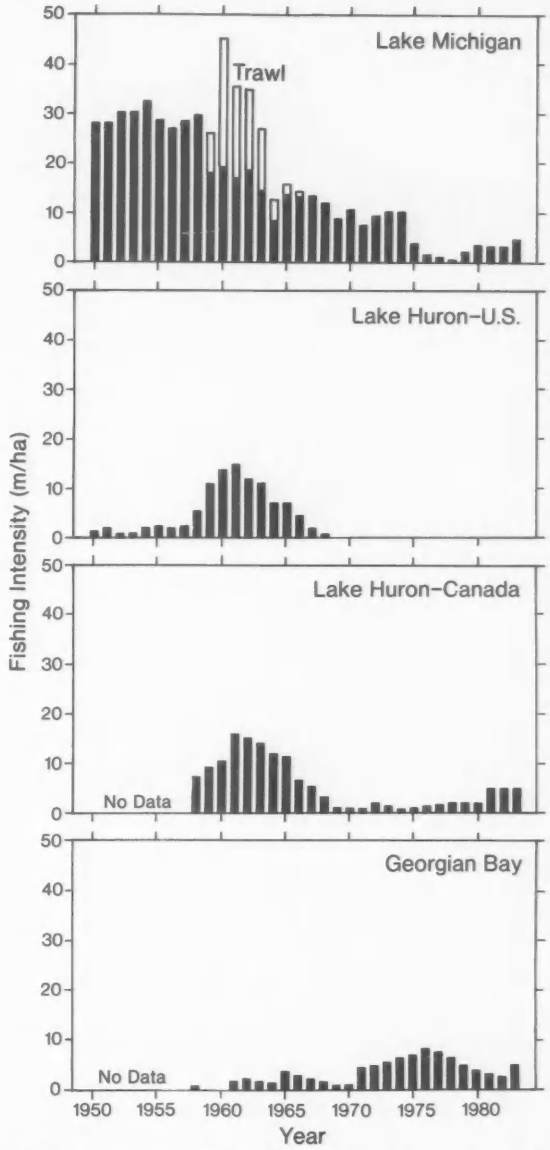

FIG. 3. Commercial fishing intensity for chubs in metres of gill net lifted per unit area of fishable habitat (water 37–110 m deep) in Lake Michigan, U.S. and Canadian waters of Lake Huron proper, and Georgian Bay, 1950–83; see text regarding trawls.

(Brown et al. 1985). Yield had climbed to an all-time high in Lake Michigan in 1960, augmented by small chubs caught in trawls for animal food, and was depressed for 1 yr or more following deaths of several people from botulism in smoked chubs in 1963 (Baldwin et al. 1979). In contrast, chub yield exceeded 1 kg/ha only briefly on the U.S. and Canadian sides of Lake Huron proper in the early 1960s and exceeded 0.5 kg/ha only once (1975) in Georgian Bay (Fig. 2).

Fishing intensity in the gillnet fisheries for chubs in Lake Michigan reached a record high in 1953, following a substantial transfer of fishing effort from severely depleted lake trout (Eschmeyer 1957) to chubs (Fig. 3). Alewives, which would increase explosively in abundance a decade later, were just becoming established throughout the lake but were not yet recognized as a potential threat to chubs (Brown 1972). Fishing intensity for chubs then declined in nearly a straight line ($r^2 = 0.86$, df = 1, 20, $p < 0.01$) through 1974, except for a short interruption following the outbreak of botulism. The decline in fishing intensity had several interrelated bioeconomic causes: e.g. depletion of the larger species of ciscoes from exploitation and sea lamprey predation, slow growth and hence low

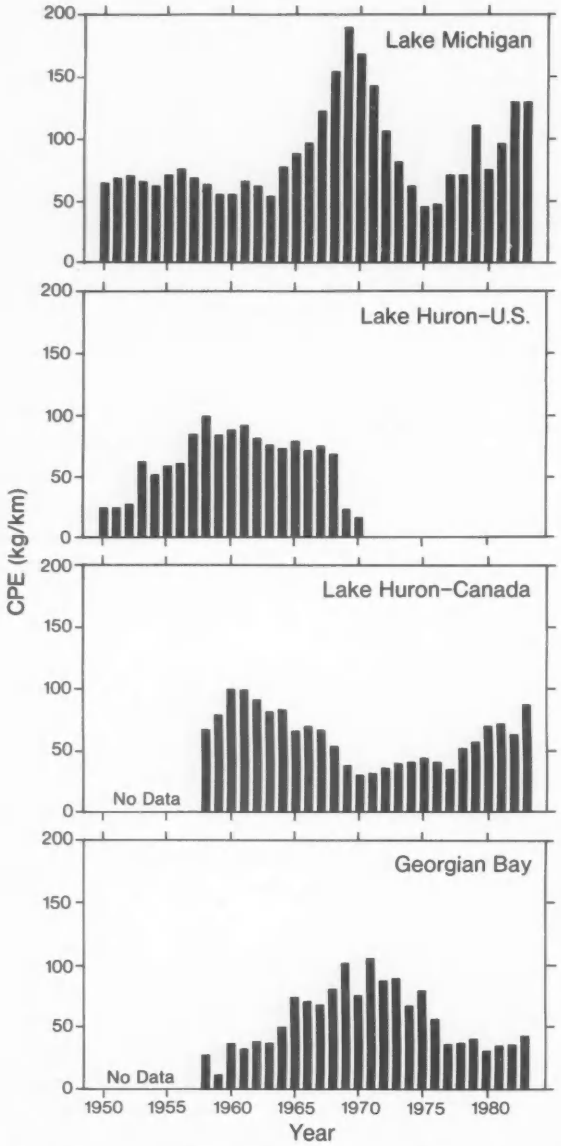

FIG. 4. Commercial catch of chubs in round weight per unit of effort (CPE) in Lake Michigan, U.S. and Canadian waters of Lake Huron proper, and Georgian Bay, 1950–83.

marketability of bloaters from over abundance after large predators (lake trout and burbot) were also depleted by sea lampreys, depressed markets, and rising operating costs (Smith 1968; Brown et al. 1985).

Fishing intensity, distantly approaching that in Lake Michigan, did not build up in Lake Huron proper until just before the alewife population crested in that lake in the early 1960s (Henderson and Brown 1985) and was short-lived as yield fell and the stocks collapsed later in the decade (Fig. 2 and 3). Michigan responded with a ban on small-mesh gill nets in U.S. waters in 1971 that is still in effect, except in waters ceded by the

TABLE 1. Estimated biomass (thousands of metric tons) of bloaters available to bottom trawls[a] in Lakes Michigan and Huron by life stage[b], spring (April–May) and fall (October–November), 1967–84; mean biomass based on multiseason sampling with a larger trawl[c] in 1963–65 is shown for comparison.

	Lake Michigan, fall		Lake Huron			
			Spring		Fall	
Year	Adults	YOY	Adults	Yearlings	Adults	YOY
1963–65	63.0	—	—	—	—	—
1967	54.5	—	—	—	—	—
1968	87.6	—	—	—	—	—
1969	57.8	—	—	—	—	—
1970	31.8	—	—	—	—	—
1971	36.7	—	—	—	—	—
1972	12.6	—	—	—	—	—
1973	9.4	<0.1	0.4	<0.1	0.2	<0.1
1974	2.8	<0.1	0.1	<0.1	0.8	<0.1
1975	2.1	<0.1	0.1	<0.1	0.4	<0.1
1976	2.0	<0.1	0.4	<0.1	0.5	<0.1
1977	2.0	<0.1	0.5	<0.1	0.8	<0.1
1978	5.9	0.5	0.4	0.1	0.4	0.1
1979	14.3	0.5	0.3	0.1	1.8	0.1
1980	37.5	1.7	1.1	0.1	1.3	0.1
1981	58.7	1.7	3.0	0.1	3.2	0.2
1982	58.7	9.1	3.3	0.2	2.9	0.6
1983	133.5	8.0	3.8	0.5	6.2	0.3
1984	161.8	8.4	10.1	0.7	5.8	0.1

[a]Semiballoon trawl with 12-m headrope used as a standard.
[b]Young-of-the-year (YOY), yearlings, and "adults" (≥age 1 in fall and age 2 in spring).
[c]Gulf of Mexico trawl with 16-m headrope.

Treaty of 1836 where a chub catch quota was recently established. The late development of significant chub fisheries in Lake Huron proper and their development about 10 yr later in Georgian Bay are explained by several factors, including competition with the very productive and strategically located chub fisheries in Lake Michigan and transfer of fishing effort from lake trout to more profitable whitefish rather than to chubs. In addition, Georgian Bay chubs traditionally had lower marketability because of darker pigmentation and poor condition compared with those in the main basin of Lake Huron.

A progressive decline in year class strength and recruitment of Lake Michigan chubs (i.e. bloaters) that resulted in loss of yield and finally the ban on fishing in 1976 was masked temporarily by extremely high CPEs in the size-selective gillnet fisheries in the late 1960s and early 1970s (Fig. 4). Modal lengths and ages of bloaters in commercial nets typically are higher than those in trawls (Brown et al. 1985), which sample a wider cross-section of the population. The gillnet selectivity and the decline in fishing intensity noted earlier, interacting with the changes in vital statistics (e.g. improving growth rate, high predominance of longer-lived, faster-growing females), account for the record high CPEs.

Although somewhat obscured by these interactions, the deteriorating state of the Lake Michigan bloater population was evident from changes in the estimated biomass fishable by survey trawls (Table 1) and from changes in CPEs of the trawls and graded-mesh gill nets at widespread locations (Keller et al. 1974; National Fisheries Center – Great Lakes, unpubl. data). The biomass of age 1 and older fish near the peak in commercial

CPE in 1970 (31 800 t) was only 36% of that in 1968 (87 600 t). It then dropped to an average low of just 2 200 t (2.5% of the 1968 estimate) in 1974–77, from which the population has made a remarkable recovery.

The Lake Michigan bloater population demonstrated great resilience in the rapidity of its recovery compared with that of the smaller population in U.S. waters of Lake Huron that has been recovering simultaneously, but from a more prolonged state of depletion (Smith 1970). The biomass of age 1 and older chubs in Lake Michigan increased 80-fold from 1977 to 1984, whereas that in Lake Huron increased less than 8-fold in the same period (Table 1). The former condition of the Lake Huron population and its slower recovery suggest a lower "domain of attraction," similar to that described by Peterman et al. (1979) for a hypothetical prey species when additional predators were added in predator-prey simulations.

Enviromental Factors Implicated in Changes in Chub Populations

Several environmental factors, including exploitation, have been linked, at least circumstantially, to the drastic changes in chub populations in Lakes Michigan and Huron in 1950–84. Because these factors affected chubs simultaneously in some periods, their individual effects tend to be confounded. Here we focus briefly on the seemingly more important factors before considering the biological responses that they may have elicited in chubs.

Fishing as a Factor in Population Collapse

Conclusive evidence showing that fishing was the dominant factor in the decline of coregonines has seldom been documented for the Great Lakes, partly because of the sequential fishing-up of individual stocks to maintain yield. When population collapse was finally evident on a regional scale, it was difficult to separate the effect of overfishing from those of various ecological changes. Selgeby (1982) argued convincingly that overfishing was the main cause of the decline of lake herring in western Lake Superior, however, and Van Oosten (1930) concluded that it was the main cause for the collapse of that species in Lake Erie in the 1920s. A synthesis group at the ASPY Conference tried unsuccessfully to use change in searching rate of fishermen to predict population decline in Lake Michigan chubs while the CPE was still being maintained by sequential fishing (M. Holey, pers. comm.).

In U.S. waters of Lake Huron during 1957–68, a general pattern of fishing intensification and increasing CPEs, followed by gradually declining CPEs, was repeated from one fishing ground to another as fishermen shifted their operations. Peaks in CPE and landings from nine major grounds occurred as much as 5 and 7 yr apart, respectively (R. Eshenroder, unpubl. report). This indication of sequential "fishing-up" of the stocks in U.S. waters would explain the sustained CPE there in the mid-1960s before its sudden drop in 1968 (Fig. 4). In Canadian waters, we found that collapse of the chub stocks began by as much as 4 yr earlier and was more precipitous in statistical districts (Hile 1962) that had the greatest fishing pressure.

The best information we could find on the direct impact of fishing on chubs came from what was probably an individual stock fished by a single fisherman to the point of collapse in an 87 800-ha area of southwestern Georgian Bay. Fishing intensity by this fisherman averaged 5.9 m/ha (range 4.4–8.3) in

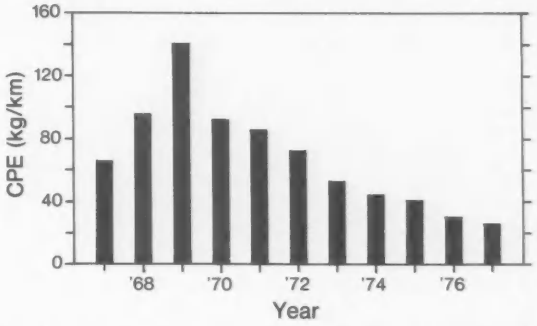

FIG. 5. Catch of chubs per unit of gill net effort by a single commercial fisherman in a small sector of southwestern Georgian Bay, 1967–77.

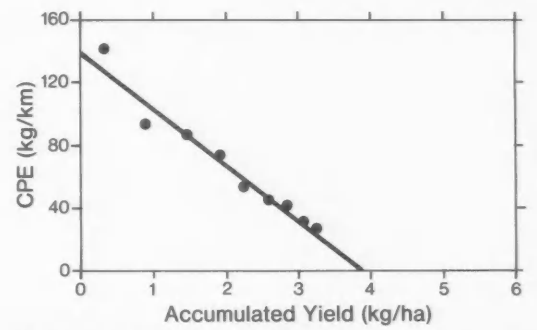

FIG. 6. Relation between chub catch per unit of gill net effort (CPE) and accumulative yield for a single commercial fisherman in a small sector of southwestern Georgian Bay, 1967–77.

1967–77 and showed no trend. His chub CPE doubled to 139 kg/km between 1967 and 1969 and then declined steadily at an average rate of 18%/yr (Fig. 5). The decline in CPE as a linear function of the accumulative yield (Fig. 6, $r = -0.98$) implies that recruitment was declining at a constant rate. Some measure of recruitment during the fishing period is provided by the quantities of "small" chubs that were sorted from the catch and marketed separately. Changes in the percentage weight of these fish in the catch paralleled changes in the total CPE, increasing to 46.3% in 1969 and then declining steadily to only 0.7% in 1976. In semilog form, that decline was also linear ($r = -0.95$) with a slope of -0.77. The decline in CPE as a function of accumulative yield was not confined to the single fisherman in Georgian Bay. In statistical district GB-2 (Hile 1962), the only other area of the bay to be fished in its entirety throughout the period of decline, CPE and accumulative yield were also highly correlated ($r = -0.91$).

To determine how intensively the single fisherman was exploiting the chub stock in southwestern Georgian Bay, we first estimated total mortality (A) between successive ages of cohorts sampled there in 1976 and 1977. These estimates ranged from 0.58 to 0.63 and averaged 0.62. We assumed that the conditional natural mortality rate (n) of 0.42 reported by Brown et al. (1985) for Lake Michigan bloaters would approximate that in Georgian Bay and thus obtained a conditional fishing mortality rate (m) of 0.35 and an exploitation rate (u) of 0.27. We then used a catchability coefficient computed on the basis of the single projection of fishing mortality to obtain u values for the

other years ranging from 0.20 to 0.33 (average 0.24). Tentatively, these moderate exploitation rates were high enough in the presence of failing recruitment to seriously deplete the stock.

The estimated fishable biomass ($\bar{B}$) that we obtained by using catch (C) and effort (f) data and the catchability coefficient q referred to above (where $C = qf\bar{B}$) declined from 3.2 kg/ha when the fishery was at its peak in 1969 to 0.6 kg/ha in 1977, the last year of fishing. Given that the size of the exploitable stock was declining at a rate roughly equal to the exploitation rate, the x-intercept (3.9 kg/ha) of the CPE – accumulative yield regression line (Fig. 6) should approximate the 1969 biomass of 3.2 kg/ha, as it appears to do.

Alewife and Rainbow Smelt as Possible Predators and Competitors

A program of yield prediction for bloater populations in Lakes Michigan and Huron would be incomplete if it did not allow for the limiting effects that alewives and rainbow smelt may exert in the future. Alewives, especially, have been strongly implicated by circumstantial evidence in the decline or disappearance of chub populations in the Great Lakes (Smith 1968, 1970). Most investigators believe that the exotic species affect chubs mainly at early life stages, but the possible mechanisms involved have been the subject of much speculation. Recently, Eck and Wells (1987) obtained a statistically significant negative correlation between the fall abundance of young-of-the-year bloaters in Lake Michigan and the abundance of older alewives.

Alewives are known to prey on the larvae of other fish species in freshwater (Kohler and Ney 1980), as well as on their own larvae (Rhodes et al. 1974), and rainbow smelt are known to prey on the young of both alewives (O'Gorman 1974) and bloaters (Stedman and Argyle 1985). Smith (1970) and Wells and McLain (1973) proposed that predation on early life stages by the exotics was a possible cause of the decline and extirpation of deepwater ciscoes and other native species in Lake Michigan. To further explore the predation hypothesis, Crowder (1980) synthesized available information on spawning habits and egg characteristics of the affected species relative to the vulnerability of their eggs and fry to potential predators.

We agree with Crowder (1980) and with Eck and Wells (1987) that predation by alewives on early life stages was likely a major factor in the declining recruitment of bloaters in the 1960s and early 1970s. Lake Michigan bloaters spawn in January–March (Emery and Brown 1978) in deep offshore waters (Wells 1966), where their semibuoyant eggs (Crowder 1980) would be vulnerable to predation by alewives that overwinter at the same depths (Wells 1968). Although the bulk of the (anadromous) alewife spawning population has moved inshore by May–July when bloater larvae hatch in the offshore areas (Wells 1966, 1968), many preadult alewives still occupy midlevels offshore where theycould prey on the emergent larvae that swim actively (Crowder et al. 1987) and are subject to transport by currents (Crowder 1980).

Although the question of competition with the exotics for a limited food resource is even more difficult to address, a number of recent new insights have been gained. Rice (1985) reported that larval bloaters are highly resistant to starvation in the laboratory, an indication that competition for food is not a critical factor in the survival of bloaters during the initial feeding stage. Crowder et al. (1987) suggested, nevertheless, that growth retardation of larval and postlarval bloaters due to zooplankton depletion by alewives and other species may indirectly affect mortality from size-dependent predation.

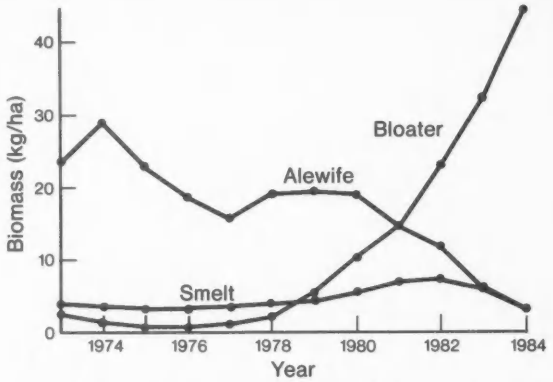

FIG. 7. Biomasses (3-yr moving averages) of bloaters, alewives, and rainbow smelt available to 12-m bottom trawls in Lake Michigan, per unit area at depths of 9–110 m, October–November 1973–84.

Alewife populations in Lakes Michigan and Huron have shown certain similarities in dynamics, but have differed considerably in rates of change and in densities attained. The alewife was first identified in Lake Huron in 1933 (Miller 1957) but apparently did not reach maximum population size there until the early 1960s, judging by its peak abundance near South Bay, Manitoulin Island, in northeastern Lake Huron in 1964 (Henderson and Brown 1985). It was not identified in Lake Michigan until 1949, but numbers there increased enormously by 1966 and a mass lakewide die-off occurred there in 1967, all in less than 20 yr (Brown 1972).

Rainbow smelt, which were planted in Crystal Lake, Michigan, in 1912 (Miller 1957), increased greatly in abundance in Lakes Michigan and Huron in the 1930s and then suffered extremely high mortality in both lakes during the winter of 1942–43 (Van Oosten 1947). Commercial catch records for smelt suggest that population density then followed a similar trend in each lake: after catches increased in the 1950s, they declined in the early 1960s, possibly because of population "pressure" from alewives. Catches in experimental gill nets in Georgian Bay showed that smelt abundance increased from 1958 through 1962 and decreased in 1963 (Ontario Ministry of Natural Resources, unpubl. data).

Planted lake trout and Pacific salmon, which have preyed mainly on alewives and smelt in Lakes Michigan and Huron, possibly modified the impact of those species on chubs, but to a different degree in each lake. Salmonine plantings of 1 million or more fish a year began in Lake Michigan in 1965, but the number planted did not reach that level in U.S. waters of Lake Huron until 1970. In 1970–81, an average of 4.1 salmonines was stocked per hectare in Lake Michigan as compared with 2.0 in Lake Huron. Although bloaters and other ciscoes were a mainstay in the diet of native lake trout before the invasion of the sea lamprey, planted trout were slow to switch from a diet of the exotic species in Lake Michigan in the 1980s (J. Kitchell, pers. comm.).

After 1973, when trawl surveys of comparable scope were first conducted concurrently in Lake Michigan and in U.S. waters of Lake Huron, trends in alewife abundance were similar in the two lakes, as were those of the rainbow smelt, but population density of each exotic, and hence its possible

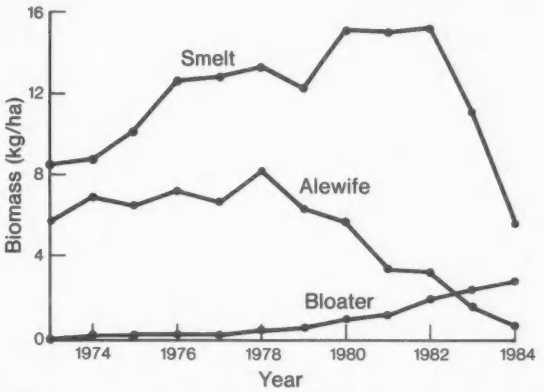

FIG. 8. Biomasses (3-yr moving averages) of bloaters, alewives, and rainbow smelt available to 12-m bottom trawls in U.S. waters of Lake Huron proper, per unit area at depths of 9–110 m, October–November 1973–84.

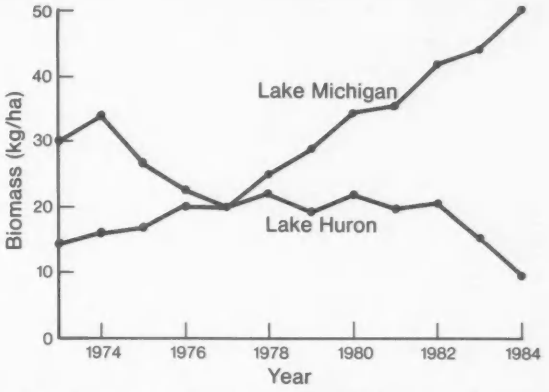

FIG. 9. Biomasses (3-yr moving averages) of bloaters, alewives, and rainbow smelt combined available to 12-m bottom trawls in Lake Michigan and in U. S. waters of Lake Huron proper, per unit area at depths of 9–110 m, October–November 1973–84.

negative impact on the bloater, has differed considerably between lakes (Fig. 7 and 8). Average annual biomass (kilograms per hectare) of alewives during 1973–84 was more than 3 times greater in Lake Michigan (17.3 kg/ha) than in Lake Huron (5.3), whereas that of smelt was more than 2.5 times greater in Lake Huron (12.0 kg/ha) than in Lake Michigan (4.6) (Fig. 7 and 8). The slower recovery of bloaters in Lake Huron, where smelt were more abundant, may indicate that a unit biomass of smelt has a greater negative effect on bloaters than a unit biomass of alewives. The sheer numbers of alewives in some periods would more than compensate, however, for their possibly lower unit impact on chubs. Because of physical limitations on the size of prey eaten, predation by alewives on bloaters would be limited primarily to bloater fry, whereas smelt could theoretically eat both fry and small fingerlings, as shown by Stedman and Argyle (1985). It may be significant, therefore, that no chubs were caught in graded-mesh gill nets in 1985 from Parry Sound, a deep embayment of Georgian Bay, where they have not been fished commercially since World War I and smelt are abundant; however, alewives are also present (Ontario Ministry of Natural Resources, unpubl. information).

Selgeby et al. (1978) estimated that rainbow smelt ate 3–11% of the larval lake herring in Black Bay of Lake Superior, where the lake herring were comparatively abundant, but concluded that smelt predation on the larvae was not an important factor in determining herring abundance. Population densities of smelt declined markedly in the early 1980s in U.S. waters of Lake Superior, however, and lake herring abundance soon increased greatly in some areas (National Fisheries Center – Great Lakes, unpubl. data).

Other Limitations

Effective sea lamprey control was attained several years later in Lake Huron than in Lake Michigan. This lag delayed trout and salmon plantings in Lake Huron and extended the period over which sea lampreys may have heavily parasitized adult bloaters in that lake. Sea lampreys continued to be more abundant in Lake Huron than in Lake Michigan in the 1980s, largely because ammocoete production was uncontrolled in the St. Marys River. This difference may explain, in part, the slower recovery rate of bloaters observed in Lake Huron.

Quantitative differences within the complex of bloaters, alewives, and smelt — and hence in the capacity of bloaters to respond to environmental change (Skud 1982) — may also have been influenced by oligotrophic differences between Lakes Michigan and Huron. Only about 60% of the surface area of Lake Michigan lies above the 44th parallel as compared with 90% of the surface area of Lake Huron (Fig. 1), and concentrations of most dissolved solids are higher in Lake Michigan (Weiler and Chawla 1969). These indications that Lake Michigan is less oligotrophic and therefore more productive would partly explain why such high commercial yields were sustained for so long in that lake (Fig. 2) and why population density of bloaters and of the two exotics combined was higher there than in Lake Huron in all reference years (1973–84) except 1977, as judged by 3-yr moving averages (Fig. 9). In some years, the combined population density was 2 or more times greater in Lake Michigan than in Lake Huron, as species abundance fluctuated and dominance shifted. Alewives were by far the dominant species in Lake Michigan until the early 1980s, when they were surpassed by bloaters. In contrast, rainbow smelt, which have a lower preferred temperature than alewives, were the dominant species in Lake Huron during the entire sampling period (1973–84) and were much more abundant than the alewife beginning in about 1976 (Fig. 7 and 8).

Population Regulation and Response of Bloaters to Environmental Change

We next examine changes in various population parameters for indications of mechanisms that regulated population size of bloaters in the two lakes. Identification of such response systems and how they may have been affected by exploitation and exotic species is another requirement for the rational prediction of yield (Koonce and Shuter 1987).

Year Class Strength, Survival, and Recruitment

Five comparatively strong year classes of bloaters were produced in Lake Michigan in 1960–64, just preceding a series of drastic population changes (Fig. 10). These year classes, in which females were strongly predominant, contributed to the exceptionally high commercial catch rates and the improved

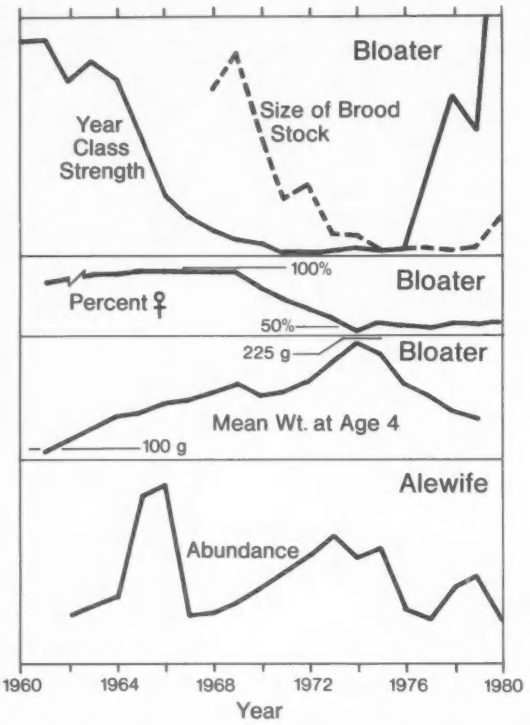

FIG. 10. Strength of 1960–80 year classes of Lake Michigan bloaters, assessed at ages 3 and 4, size of brood stock from previous fall; percent female in fishable stock; age 4 mean weight of year class; and adult alewife (≥age 2) abundance, including 1962–66 values adapted from Wells (1985): fall trawl data, showing only relative changes in abundance.

yields that peaked in 1968–70 (Fig. 3 and 4). The strength of succeeding year classes, estimated by their accumulative standing stocks available to trawls at ages 3 and 4 in fall, then (1965) began a precipitous decline that reached extremely low levels by the early 1970s and improved little through 1976 (Fig. 10). (Comparative strengths of the 1960–63 year classes above were computed as relative values (Wells and Brown 1974) times the ratio of accumulative values to relative values in 1964, a year of overlap in the data series.) During the decline in bloater year class strength, alewife abundance oscillated sharply in Lake Michigan, climbing to a record high in 1965–66, plummeting during the mass die-off in 1967, and slowly rising to a secondary plateau that extended from about 1973 to 1975 (Fig. 10).

Environmental conditions, including a drop in alewife abundance in 1977, apparently were optimal again for Lake Michigan bloaters in the late 1970s. The young produced by the very small adult stocks (Fig. 10) began generating a remarkable growth in population size that continued into the early 1980s. The turning point for the survival of young bloaters was in 1977, as indicated by relative survival from theoretical egg production of the lakewide standing stock each year (1974–84) to the estimated stocks of young-of-the-year bloaters in fall (Table 2). The relative survival rate increased roughly 25 times from 1976 to 1977 and averaged 25 times higher in 1977–84 than in 1974–76.

TABLE 2. Relative survival[a] of Lake Michigan bloaters from the estimated number (millions) of eggs available for deposition in January–March[b] to the estimated number (thousands) of young-of-the-year (YOY) available to bottom trawls in October–November, 1974–84.

	Number		
Year	Eggs	YOY	Survival rate
1974	303 869	11 712	0.000039
1975	79 317	2 953	0.000037
1976	65 981	1 149	0.000017
1977	63 231	27 322	0.000432
1978	70 745	73 939	0.001045
1979	157 528	85 478	0.000543
1980	385 891	527 884	0.001368
1981	1 208 699	439 075	0.000363
1982	2 175 644	1 899 462	0.000873
1983	1 616 548	1 882 521	0.001164
1984	3 131 196	1 511 007	0.000483

[a]Relative because female reproductive stock on which egg production was based and YOY may not be sampled with equal efficiency by the trawls.

[b]Based on size-specific fecundity (Emery and Brown 1978) of age groups in the female reproductive stock in the preceding fall (i.e. 1973–83).

Bloater survival also improved in U.S. waters of Lake Huron in 1977, when stocks that had been much more severely depressed than those of Lake Michigan since the mid-1960s produced a year class 17 times stronger than the mean for 1973–76 (based on the trawl CPE at age 0). Year class strength changed little in U.S. waters through 1980, but increased by a factor of 9 from 1980 to 1982 (Lake Huron Chub Technical Committee 1984).

The winter of 1976–77 was extremely severe throughout the Great Lakes and potentially stressful for alewives, as were several that followed (Eck and Brown 1985). Subsequently, heavy alewife die-offs attributed to cold stress were reported for southwestern Lake Michigan, South Bay of Lake Huron (J. Rekhan, pers. comm.), and all of Lake Ontario (O'Gorman and Schneider 1986; J. Christie, pers. comm.).

We found no evidence of a functional relation (e.g. Ricker or Beverton and Holt types) between the estimated number of Lake Michigan bloaters when fully recruited at about age 3 or 4 to the fishable stock available to trawls and the number of parents in fall before the seasons (1968–79) in which the recruits were hatched (Fig. 11). A stock-recruitment relation may have been suppressed by reproductive inefficiency of bloaters resulting from the strong predominance of females in the 1960s and early 1970s (Brown et al. 1985; and Fig. 10) and by species interactions,especially the inferred predation by alewives on bloater fry. Interspecific effects on population density have also been suggested as the reason why some subordinate marine species have not shown stock-recruitment relations (Skud 1982).

Growth, Maturity, and Fecundity

Lake Michigan bloaters exhibited a series of classic density-dependent growth changes beginning in the 1950s (Brown

TABLE 3. Average length (mm) at different ages of chubs taken in bottom trawls or graded-mesh gill nets in Lake Michigan, U.S. waters of Lake Huron, and Georgian Bay in various periods, 1961–84; number of fish in parentheses.

	Bottom trawl		Graded-mesh gill net, Georgian Bay		
Age	Lake Michigan, Oct.–Nov. 1980–83	Lake Huron[a], Aug.–Sept. 1980–83	Aug.–Sept. 1980–83	Aug.–Sept. 1971–84	July–Aug. 1961
1	152 (745)	142 (68)	194 (11)	180 (60)	—
2	198 (1345)	172 (113)	216 (671)	219 (1153)	—
3	233 (1231)	207 (138)	258 (190)	259 (756)	—
4	253 (388)	239 (138)	292 (75)	283 (537)	225 (4)
5	276 (78)	275 (109)	331 (13)	305 (248)	236 (26)
6	309 (23)	304 (59)	—	320 (141)	242 (28)
7	318 (6)	315 (63)	—	331 (44)	249 (27)
8	320 (3)	336 (72)	—	—	262 (19)
9	—	360 (48)	—	—	262 (13)

[a]Includes some fish from graded-mesh gill nets.

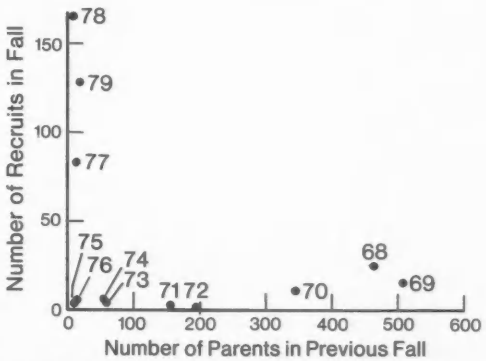

FIG. 11. Relation between number of bloater recruits fishable by trawls in Lake Michigan, taken as average cohort size at ages 3 and 4 in fall 1971–72 through 1982–83, and their potential parents ≥age 2 prior to given year hatched.

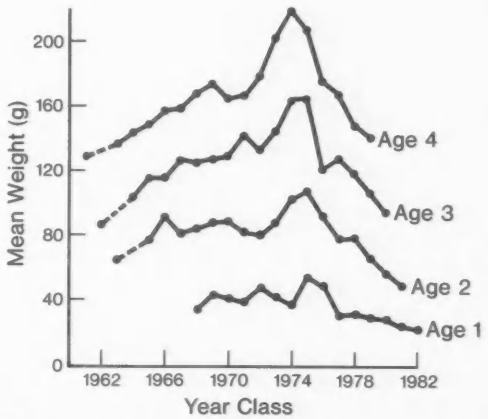

FIG. 12. Change in mean weight at capture, by age group, of bloaters from year classes 1962–82 taken in bottom trawls in Lake Michigan, October–November 1965 and 1967–83.

1970). Growth was severely depressed in the mid-1950s after the destruction of large predators by sea lampreys and the depletion of large species of chubs by selective fishing and lamprey predation (Smith 1968; Brown 1970). Bloaters filled niches vacated by the larger species (Smith 1964), and may have undergone a moderate population explosion of their own, judging by their slow growth and by the unusual numbers of dead fish observed in some areas (L. Wells, pers. comm.). Growth of the bloater then followed a generally upward trend from the early 1960s through about 1978, as indicated by mean weights of fish of the various year classes at ages 1–4 (Fig. 10 and 12). It then dropped markedly because of the increase in size and rejuvenation of the population that continued into the 1980s.

Mean lengths and weights of bloaters sampled in various years during the growing season in Lake Huron proper and Georgian Bay provided only rough comparisons with those of Lake Michigan bloaters collected at or near the end of the growing season. The fact that some of the midseason samples were obtained with graded-mesh gill nets rather than with trawls signals further caution, because the gill nets may have selected somewhat larger fish (Brown et al. 1985). Tentatively, then, it appears that growth in length — a more conservative statistic than weight — in Lake Huron proper in 1980–83 was less than or about equal to that in Lake Michigan, if allowance is made for length increments to be added in Lake Huron in late summer and fall (Table 3).

The rate of growth in length of bloaters in Georgian Bay in 1980–83 appears to have been faster than that in Lake Michigan and Lake Huron proper, despite sampling bias from mid-season sampling and size-selective gear. The fast growth rate in Georgian Bay in the 1970s and 1980s contrasts markedly with the extremely slow growth indicated for 1961 (Table 3), suggesting that population density was much higher in the bay in the early 1960s than in 1971 and later.

Despite the pronounced changes in growth in the Lake Michigan population, no inverse relation was evident between growth rate and age at maturity, as judged by a long series of maturity data (1967–83) for fish from the southern half of the lake. For the 17 yr combined, an average (weighted by year) of 18% of the age 1 females and 47% of the age 1 males were sexually mature and would spawn in the following winter, compared with 93% of the age 2 females, 97% of the age 2 males, and 99% or more of all older fish.

A decrease in fecundity of Lake Michigan bloaters, resulting from the drastic drop in mean weight-at-age after about 1977

TABLE 4. Fecundity (F)[a] and number of eggs ($E \times 10^6$) contained in the estimated stock of mature female bloaters (N)[b] available to bottom trawls in Lake Michigan in fall 1973–83.

Year	Statistic[c]	Reproductive statistic by age group								
		1	2	3	4	5	6	7	8	Total
1973	*F*	3 996	5 939	8 647	11 356	14 064	16 251	22 661	27 489	—
	E	208	18 524	93 517	98 388	52 037	19 566	19 628	4 701	303 869
1974	*F*	2 583	4 761	9 943	10 943	14 064	19 540	21 424	29 962	—
	E	1 868	3 028	17 639	22 827	20 140	7 308	4 649	1 858	79 317
1975	*F*	2 759	6 351	8 824	12 121	16 184	13 063	16 360	22 484	—
	E	1 912	20 971	14 030	10 509	13 578	3 396	933	652	65 981
1976	*F*	3 112	6 241	9 589	12 533	16 007	22 661	19 246	—	—
	E	377	16 389	30 263	7 821	3 522	4 147	712	—	63 231
1977	*F*	3 937	6 771	10 296	14 241	19 481	18 951	21 719	—	—
	E	217	6 588	31 578	23 968	3 838	2 123	2 433	—	70 745
1978	*F*	2 347	4 938	10 414	14 653	16 890	20 011	29 903	29 962	—
	E	8 719	4 864	21 859	67 814	41 533	6 243	2 871	3 625	157 528
1979	*F*	2 347	5 409	7 293	14 241	19 422	21 365	30 786	—	—
	E	24 512	250 242	19 538	32 526	26 802	21 557	10 714	—	385 891
1980	*F*	2 288	5 468	8 353	11 356	20 364	26 606	27 842	—	—
	E	35 526	536 914	504 914	45 481	43 212	35 998	6 654	—	1 208 699
1981	*F*	2 347	4 526	7 941	10 767	13 004	40 619	17 067	27 901	—
	E	96 793	553 294	1 161 427	294 682	40 546	21 122	2 953	4 827	2 175 644
1982	*F*	2 053	3 937	6 999	9 471	11 650	12 298	24 427	32 965	—
	E	74 620	787 723	438 060	265 453	39 284	8 424	1 270	1 714	1 616 548
1983	*F*	1 935	3 525	6 469	9 354	10 943	12 357	—	13 829	—
	E	407 461	706 255	1 228 573	673 048	101 529	11 702	—	2 628	3 131 196

[a]Number of eggs per female weighing W grams, where $F = 580.6 + 58.88W$ (Emery and Brown 1978).
[b]Number of females that would spawn in the following winter.
[c]$E = FN \times 10^{-6}$.

(Fig. 12), averaged 44% among fish of ages 1–5 (unweighted mean), based on a fecundity – body weight relation of 1968–69 (Emery and Brown 1978). The negative effect of this decrease on theoretical egg production was far offset, however, by the large increase in year class strength in the 1980s (Table 4).

Sex Composition

The most enigmatic feature of the population dynamics of the bloater in Lake Michigan was the development of extreme female predominance when bloaters were still abundant in the 1960s, followed by a smooth transition to more balanced sex ratios in weaker year classes hatched during and after the major alewife die-off in 1967 (Brown 1970; and Tables 5 and 6). Females were also strongly predominant in the two earliest, temporally separated collections of chubs from U.S. waters of Lake Huron (85%) and Georgian Bay (83%), and the sex ratios in Lake Huron have taken on lower values in recent years as they have in Lake Michigan (Table 5). Reminiscent of what occurred earlier in Lake Michigan, the percentage of females caught in the late-peaking commercial fishery for bloaters in Georgian Bay declined progressively from 87% in 1970–71 to 56% in 1978–79, a period in which the commercial CPE peaked and then declined to below 50 kg/km (Fig. 4). The change in percentage female was not as apparent, however, among chubs taken in graded-mesh gill nets from Georgian Bay during 1970–83 (Table 5). Either the graded mesh took younger chubs for which the sex ratio had already shifted, or the commercial catches were biased by selection for longer-lived females on the basis of size.

A strong predominance of females in periods of high population density and subsequent decline was reported for the lake herring in Birch Lake, Michigan (Clady 1967), as well as for the Lake Michigan bloater (Smith 1968; Brown 1970). George (1977a) suggested that the change in sex ratio in coregonines is under the control of the neuroendocrine system and represents a response to changes in intraspecific and possibly interspecific population density. Brown et al. (1985) noted that the change in sex ratio in Lake Michigan bloaters after the 1967 alewife die-off may have been more than coincidental (Table 6).

We hypothesize that a shift in sex composition strongly favoring females is an intrinsic means by which population density is regulated in the bloater. This form of population control may be necessary if bloater larvae are as resistant to starvation as reported by Rice (1985). But regardless of the conditions that actually trigger or cause the change in sex ratio during high population density, the reproductive inefficiency that results is the proposed mechanism that reduces population size. Egg-bound female bloaters, indicating lack of spawning opportunity, were common in Lake Michigan after spawning seasons in the 1960s (National Fisheries Center – Great Lakes, unpubl. information). Also, for example, only three ripe males were collected with many hundreds of ripe and gravid females while spawn for a special study was being obtained off Kenosha, Wisconsin, in February 1969 (Brown 1970).

TABLE 5. Percent females in chub catches with various gears from Lake Michigan, U.S. and Canadian waters of Lake Huron proper, and Georgian Bay by various 2-yr intervals in 1954–83; number of fish in parentheses.

		Lake Huron proper		Georgian Bay	
Years	Lake Michigan trawl	U.S., trawl	Canada, commercial gill net	Commercial gill net	Graded-mesh gill net
1954–55	73 (6012)[a]	—	—	—	—
1960–61	89 (670)[a]	—	—	—	83 (1975)
1962–63	95 (1813)[a]	—	—	—	—
1964–65	95 (5081)[a]	—	—	—	—
1966–67	97 (6420)[a]	—	—	—	—
1968–69	96 (5909)[a]	85 (74)[b]	—	—	—
1970–71	78 (1889)	—	—	87 (530)	57 (160)
1972–73	60 (933)	52 (21)	—	—	—
1974–75	49 (904)	69 (65)	—	81 (200)	65 (666)
1976–77	50 (386)	55 (99)	60 (658)	69 (3927)	59 (455)
1978–79	53 (1594)	52 (260)	59 (1111)	56 (2303)	54 (351)
1980–81	54 (2260)	55 (620)	66 (1054)	60 (735)	59 (390)
1982–83	52 (1677)	48 (593)	71 (980)	63 (1036)	57 (321)

[a]Data from Brown (1970).
[b]Data from Smith (1970).

The reduction in numbers of live eggs deposited and fertilized and the resulting decrease in potential bloater abundance following a shift to high female predominance would be determined by the average number of females that each male spawns with effectively compared with the number of females per male in the adult population. However, the effective spawning sex ratio and change in abundance would be influenced by other reproductive and population characteristics, such as length of time that each sex remains on the spawning grounds, whether effective spawning aggregations consist of more than one male per female, age structure of the spawning population, and its fecundity. Little is known about spawning behavior of the bloater, except that it spawns in offshore waters in winter, apparently near, but not necessarily on, the bottom. Koelz (1929) observed that two to four bloaters were often gilled side by side in commercial nets set on bottom during the spawning season, and may have been captured in the act of spawning. Most bloater larvae recorded by Wells (1966) in systematic sampling with 1-m tow nets were taken from mid-May through July in the lower 18 m of the water column, over bottom depths of 73 m and greater in Lake Michigan.

If the above hypothesis is valid, the current upsurge in bloater abundance in Lake Michigan should be followed by a progressive shift to higher proportions of females in the population in the late 1980s. Failure of this phenomenon to recur would suggest that it was caused by some unusual condition or set of conditions, such as stress-induced change in the primary sex ratio triggered by population pressure from superabundant alewives, differential predation on the sexes by alewives, the reported introgression of bloaters with lake herring or other species of ciscoes that were rapidly disappearing (Smith 1964), as suggested by G. Svärdson and W. Nüman (pers. comm.), or differences in tolerance of the sexes to some formerly prevalent chemical contaminant. George (1977b) presented preliminary information which suggested that an unknown toxic substance was affecting the cisco population of Lake George differentially by sex, contributing to an 85% predominance of females.

A Synthesis of Population Regulation and Response

We conclude that resilience in bloater stocks depends partly on stock history and stock condition. Stocks that, in the absence of predation (i.e. destruction of lake trout and burbot by sea lampreys) or possibly fishing, have developed highly unbalanced sex ratios, appear to have low resilience, and may fail when fishing is continuously applied, even at seemingly low exploitation rates. These stocks are unable to compensate for renewed or increased harvesting because extreme female predominance, which appears to limit reproduction, can be changed only through the reproductive process over one or more generations (Table 6). Under stable ecological conditions, bloaters would be controlled by predation and the population would be attuned to replacing annual losses to predation with production. A carefully established fishery could also produce a similar state in which annual yield was offset by annual production.

When nonendemic species enter the community, bloater populations may be destabilized in several ways: by the sudden removal of predators, leading to the loss of resilience noted above; by the imposition of new "forms" of predation (i.e. alewives and rainbow smelt preying on early life stages of chubs); or by competition for food or space between bloaters and the invading species.

Management Implications in Predicting Yields

Although we did not quantify net production, per se, for Lake Michigan and Lake Huron bloaters, the courses of the fisheries indicate that, at a given stock size, production was low during periods of decline and high during periods of recovery. Walters (1987) referred to this pattern in the stock–production relation as a "loop," stating that in such situations, stock size alone is not a good predictor of surplus production. Our suggestion that female predominance resulting from high population density suppresses recruitment is one explanation for such a loop pattern

TABLE 6. Changes in percent females in the 1960–80 year classes of Lake Michigan bloaters at ages 2 and 3 in fall or 3 and 4 in spring in comparison with changes in that statistic in the entire fishable stock; bottom trawl surveys in various regions of the lake in 1960–61 and 1963–83; number of fish in parentheses.

Year class	Specified ages[a]	Fishable stock[b]
1960	92 (305)[c]	92 (200)[e]
1961	97 (648)[c]	88 (470)[e]
1962	97 (234)[c]	—
1963	96 (162)[c]	95 (1813)[e]
1964	97 (293)[d]	94 (3765)[e]
1965	97 (303)	97 (1316)[e]
1966	98 (225)	97 (1468)[e]
1967	85 (170)	97 (4952)[e]
1968	65 (258)	97 (3363)[e]
1969	52 (228)	95 (2546)[e]
1970	48 (170)	83 (957)[d]
1971	42 (53)	73 (932)
1972	59 (46)	66 (366)
1973	53 (105)	57 (567)
1974	49 (104)	47 (562)
1975	35 (34)	52 (342)
1976	52 (23)	51 (208)
1977	57 (449)	49 (178)
1978	51 (481)	54 (524)
1979	46 (335)	53 (1070)
1980	48 (262)	54 (1053)

[a]Weighted mean.

[b]Present in given index year of year class.

[c]Spring samples, southeast sector (Brown 1970).

[d]This and following entries fall samples, southern half of lake.

[e]Samples from different seasons and regions combined (Brown 1970).

in the stock–production relation for bloaters. If the rate at which the sex ratio reverts to a more balanced value is retarded by the turnover rate, recruitment and hence production changes would lag behind density changes. Sex ratio and its direction of change appear, therefore, to be important qualifiers when surplus production is estimated from stock size.

Fishery managers in the Great Lakes face the difficult problem of maintaining bloater yields within safe (and probably narrow) limits. To be avoided, on one extreme, is the very high population density that appears to stimulate female predominance and an accompanying loss of resilience, and on the other extreme, the possible loss at low population density of any competitive advantage by bloaters over alewives and rainbow smelt. Some combination of salmonine predators attuned to preying on preadult chubs, in harmony with moderate exploitation of the adults, would reduce the danger of overpopulation. But if sexual imbalance develops or alewives make a strong recovery, bloater harvests should be adjusted promptly to conservative levels. The task of managing bloaters is complicated by the kind of uncertainties (e.g. changing stock performance and species interactions) that Walters (1987) addresses.

Evidence that alewives and rainbow smelt can limit bloater production is convincing. For this reason, agency efforts to monitor all three species should be continued and strengthened. In this respect, hydroacoustic survey techniques, combined with present assessment methods, would seem to have much potential for improving data quality and reliability. The evidence of species interaction also gives strong support to those who favor multispecies production models. The simplicity of the deepwater community makes the modeling approach attractive, although the possible interactions would be extremely difficult to quantify.

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Forecasting Forage Demand and Yield of Sterile Chinook Salmon (*Oncorhynchus tshawytscha*) in Lake Michigan

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Kitchell, J. F., and S. W. Hewett. 1987. Forecasting forage demand and yield of sterile chinook salmon (*Oncorhynchus tshawytscha*) in Lake Michigan. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 384–389.

We assessed the potential role of sterile chinook salmon (*Oncorhynchus tshawytscha*) as piscivores and as the focus of a new trophy fishery in Lake Michigan. An energetics model for standard (not sterilized) chinook salmon was modified to extend the life history for up to 10 yr of life in Lake Michigan. A stocking of sterile fish consumes about one and a half times as much forage as would an equivalent stocking of standard chinook salmon over their life span, yet actually contributes less to the fishery because it lacks components that would mature precociously. At current growth rates, fish of trophy size (22.7 kg) would begin to appear in the fishery about 5 yr after stocking. Approximately 0.3% of sterile chinook would appear in the trophy fishery. These unique fish offer important opportunities for socioeconomic and ecological research.

Les auteurs évaluent le rôle potentiel de saumons quinnats (*Oncorhynchus tshawytscha*) stériles comme poissons piscivores et comme l'objet d'une nouvelle pêche à trophée dans le lac Michigan. Ils ont modifié un modèle de l'énergétique du saumon quinnat non stérilisé afin de prolonger le cycle vital dans le lac Michigan jusqu'à 10 a. Les poissons stériles ensemencés consomment environ 1,5 fois plus de nourriture que le même nombre de saumons quinnats non stérilisés pendant leur vie mais, en réalité, ces poissons stériles contribuent moins à la pêche car aucun individu à maturité précoce n'est présent. Au taux actuel de croissance, les poissons trophées (22,7 kg) ne seront capturables que 5 ans après l'ensemencement. Environ 0,3 % de quinnats stériles seront l'objet d'une pêche à trophée. Ces poissons uniques offrent d'importantes possibilités de recherche socio-économique et écologique.

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During the past two decades, stocking of salmonines has fostered development of a tremendously popular sport fishery in the Great Lakes. The predator–prey systems in these lakes are now dominated by interactions among a suite of exotic species. In Lake Michigan, alewife (*Alosa psuedoharengus*) serves as the primary prey for a variety of trout and salmon species whose populations are largely determined by the stocking policies of the states bordering the lake. The predator–prey systems in the Great Lakes currently lack the usual feedback between predator and prey population abundances. Although these systems are highly artificial and thus less likely to be predictable, there exists tremendous potential for intensive management and manipulation that can sustain and perhaps increase the yields of desired species.

Among the most recent potential manipulations is the prospect that large numbers of juvenile Pacific salmon might be sterilized in hatcheries before stocking (Hunter and Donaldson 1983). These fish would not undergo sexual maturation; thus they would continue to feed and grow for an indeterminate number of years beyond the typical life span of semelparous adults. The management goal of stocking sterile salmon is to foster the development of a limited trophy fishery for 22.7 kg. (50 lb) or larger salmon. The state of Wisconsin stocked 80 000 sterilized chinook salmon (*Oncorhynchus tshawytscha*) in Lake Michigan during the spring of 1986 and intends to stock 100 000 sterilized chinook salmon annually (M. Hansen, Wisconsin Department of Natural Resources, Madison, WI, pers. comm.). The state of Michigan plans a similar program (Husar 1985) and initiated it by stocking approximately 25 000 sterile chinook in 1986.

The forage base that supports stocked salmonines is finite, yet the capacity for expanded predator populations has been largely dictated by constraints to growth of the hatchery systems. Several years ago, Stewart et al. (1981) cautioned that the increasing stocking rates and resultant predatory inertia in Lake Michigan were likely to cause a decline in the abundance of alewife, the primary prey of all stocked salmonines (Hagar 1984). Recent observations support that forecast; alewife are now a fraction of their former abundance and their decrease has accompanied and perhaps caused a number of ecological changes in Lake Michigan's food web (Jude and Tesar 1985; Kitchell and Crowder 1986; Crowder et al. 1987). In response to the recent decline in alewife abundance, the states of Michigan and Wisconsin have instituted restrictions on their salmonine stocking policies. The alewife is now regarded as a vital resource in Lake Michigan.

How will the intended stocking of sterile salmon alter total demand on the alewife as a forage base? What compensations in stocking policy can accommodate the longer life and greater size of the sterile salmon? This paper addresses those questions through extension of the modeling approach used by Stewart et al. (1981). Based on simulated cohorts of 100 000 sterile fish,

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we estimate the abundance and sizes of salmon available to the future sport fishery and compare the forage base impact of a cohort of sterile fish with that of a cohort of standard, nonsterilized fish. In keeping with the spirit and intent of the International Symposium on Assessment of Stocks and Prediction of Yields, we offer our analyses and forecasts as testable hypotheses.

Methods

The Model

This analysis is derived from the bioenergetics-based modeling approach developed by Kitchell et al. (1977). Stewart (1980) extended that approach to derive estimates of total previous and anticipated predation by salmon and trout species stocked in Lake Michigan. The general assumptions of that model are presented in Stewart et al. (1981) and specific details of its application to lake trout (*Salvelinus namaycush*) are given in Stewart et al. (1983). Rice and Cochran (1984) provided an empirical evaluation of energetics modeling as an independent estimator of total predation. Kitchell (1983) discussed the importance of assumptions made in developing and applying energetics models.

Briefly restated, energetics models are derived from a balanced energy budget for individual fish based on a known or estimted growth rate, thermal history, and diet. Ontogenetic changes in diet composition and energy density of both predator and prey species are combined with estimates of mortality rates to develop an evaluation of total predation by members of a stocked cohort. As described in Stewart et al. (1981), the total lifetime consumption by members of a cohort can be calculated by estimating the rates of consumption necessary to fit the observed (or predicted) growth.

For the purposes of this analysis, we made some minor modifications to the model developed by Stewart et al. (1981) and then extrapolated the life span of salmon beyond that of the currently semelparous adult. In other words, we extended the life span in ways that would be most likely if the sterilization process simply prevented salmon from dying due to the complex processes associated with sexual maturation and spawning migrations. We will use the term "standard" chinook salmon to refer to the normal, nonsterilized chinook salmon that have been historically stocked in the Great Lakes.

Modifications of the Model

The original models used alewife caloric density information from Yeo (1978) to provide an annual pattern of energy density changes in the primary prey. We used the more complete and recent information provided by Stewart and Binkowski (1986) for the annual energy density cycles in both young-of-the-year and adult alewife. Diet proportions and energy densities of all other prey were as described by Stewart et al. (1981). Diets for years beyond those of the standard life span were assumed to be the same as the diets of standard fish during their last year of life.

The relationship between energy density and body weight in chinook salmon was linear in the original model. This regression gave unrealistically high energy densities when we extrapolated the growth rates to very large fish. We used the same linear dependence up to a maximum density of 3000 cal·g wet weight^{-1}, which is reached at about 10 kg wet weight. This is the highest energy density observed in a study of ontogenetic changes in lake trout caloric densities (Stewart et al. 1983).

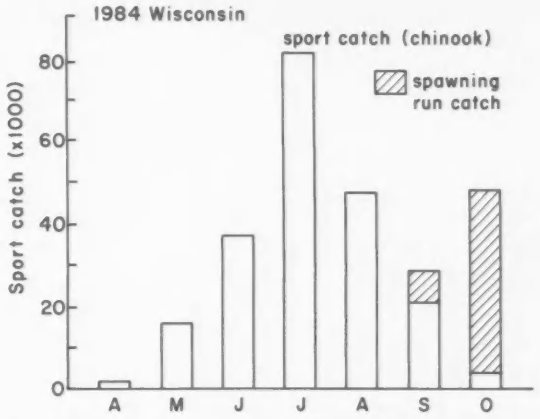

FIG. 1. Monthly distribution of total chinook salmon catches in boat, shore, and stream fisheries of Wisconsin during 1984. Catches were estimated from the reports of Bleser and Hansen (1985a, 1985b, 1985c) as the basis for estimating monthly fishing mortality rates used in model simulations.

Mortality and growth rates of chinook salmon in Lake Michigan were taken from Stewart et al. (1981, table 3). Natural mortality was assumed to be 52%·yr^{-1} for the first 2 yr in the lake and 50% thereafter (Stewart et al. 1981). Currently, return to the sport fishery is approximately 10% of salmon stocked (Wisconsin Department of Natural Resources 1986). We combined the reports of boat, shore, and stream fisheries compiled by Bleser and Hansen (1985a, 1985b, 1985c) to calculate monthly proportions of total fishing mortality. In the Pacific, sterile salmon do not make an onshore migration as do the typical spawning adults (Carl Walters, University of British Columbia, Vancouver, B.C. pers. comm.). We assumed that sterile fish were not susceptible to the spawning run fishery, and the standard fishing mortality schedules were adjusted to reflect lower exploitation in the autumn months for sterile fish (Fig. 1). Since we have no information on how susceptibility to fishing might change with increased age and size for the sterile salmon, we have assumed fishing and natural mortality rates to be constant for all years beyond the fourth year of life.

Standard stocked chinook salmon mature at different rates. Stewart et al. (1981) assumed that chinook salmon spawned in either their second (12%), third (29%), or fourth (59%) year in the lake. Precocious individuals grow at faster rates. Our model for standard chinook salmon incorporate these three groups, each with different growth rates (Table 1).

We based our extrapolation of size at age for sterile salmon on the estimates of size at age for salmon maturing during their fourth year of life in the lake (Stewart et al. 1981). These salmon have slower growth rates than those precocious individuals maturing during earlier years of life, and may more closely approximate the reduced growth rates more recently observed for all salmonines in Lake Michigan (Hagar 1984). We transformed weights at age to total body calories at age. By regressing the natural logarithm of (total calories at age $(x + 1)$ divided by total calories at age (x)) against age, we estimated successive ratios of total body calories for the extended life span of sterile salmon. We then converted total body calories into weight estimates for chinook salmon for up to 10 yr of life in Lake Michigan (Table 2). Restated, we estimated the growth curve for sterilized chinook salmon by extrapolating the

TABLE 1. Growth and survivorship data for a cohort of 10^5 standard (not sterilized) chinook salmon. Standard chinook are split into three groups: fast-growing jacks spawning during the second year in the lake, slower-growing fish spawning in the third year in the lake, and slow-growing fish spawning in the fourth year in the lake. Consumption is total cumulative kilograms consumed. Growth efficiencies are based on weights. *P* is the proportion of maximum consumption estimated by the model to produce the observed or predicted growth. The initial day of simulation is May 1 with fish stocked at 4.54 g. The final day of simulation is December 1 of the spawning year.

Age (yr)	Initial numbers	Final weight (kg)	Consumption (kg)	Growth efficiency (%)	*P*
		2-yr spawners			
1	12 163	0.49	1.8	28	0.80
2	5 548	2.64	7.4	36	0.63
		3-yr spawners			
1	29 278	0.36	1.3	28	0.69
2	14 090	2.15	6.7	32	0.63
3	6 781	7.18	24.6	29	0.74
		4-yr spawners			
1	58 559	0.23	0.9	27	0.63
2	28 182	1.55	4.7	33	0.49
3	13 563	5.91	21.7	27	0.74
4	6 675	10.36	43.8	24	0.67

observed rate of change in total body calories for salmon with a typical life span.

Initial conditions for all simulations were patterned to represent current stocking practices. Chinook salmon become smolt and are stocked about 6 mo after hatching (roughly May 1) at a weight of about 4.5 g. Throughout this report, years in the lake will be used as the reference for comparison and the independent variable. For comparison purposes, we have modeled 100 000 stocked fish for both sterile and normal chinook salmon. The Wisconsin Department of Natural Resources is currently planning on stocking 100 000 sterile chinook, and has been stocking 2.5–3 million standard chinook annually (Wisconsin Department of Natural Resources 1986).

Results and Discussion

Potential Growth Responses

One of the key parameters in energetics modeling is *P*, the proportion of maximum feeding rate that is observed for any given growth rate. In a typical application of energetics modeling, initial and final weights will be known for some time interval. In that case, the energetics model is used to estimate that proportion of maximum feeding rates resulting in the observed growth. That proportion can then be used to estimate consumption over the interval in question. Another approach is to start at a given weight and use different estimates of *P* to estimate final weight. We have used this approach to simulate the growth potential for sterile salmon in Lake Michigan, using values of *P* ranging from 0.3 to 0.9 (Fig. 2).

The annual growth pattern includes rapid growth during summer and fall followed by modest weight gains or losses during winter periods. The seasonal growth rate changes are amplified at larger size and greater age (Fig. 2). This pattern is commensurate with the energetics constraints on growth report-

TABLE 2. Growth and survivorship data for a cohort of 10^5 sterile chinook salmon. Columns are as described in Table 1.

Age (yr)	Initial numbers	Final weight (kg)	Consumption (kg)	Growth efficiency (%)	*P*
1	100 000	0.23	0.9	27	0.63
2	48 000	1.55	4.7	33	0.49
3	22 611	5.91	21.7	27	0.74
4	8 876	12.67	56.3	23	0.77
5	2 623	22.42	108.7	21	0.72
6	775	31.84	174.0	18	0.65
7	229	39.75	246.8	16	0.59
8	68	45.01	323.4	14	0.55
9	20	49.06	402.9	12	0.52
10	6	51.51	482.8	11	0.50

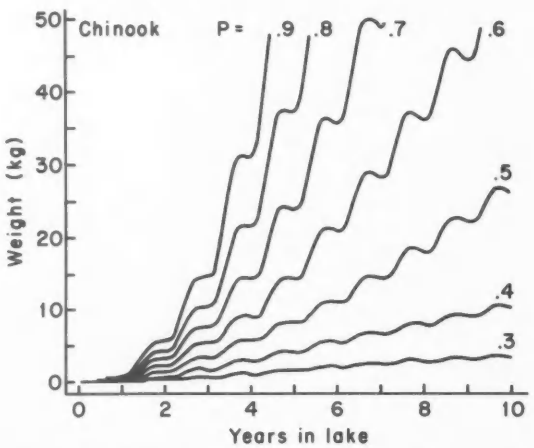

FIG. 2. Potential growth curves for sterile chinook salmon in Lake Michigan. *P* represents the proportion of maximum consumption in the simulation.

ed by Stewart et al. (1983) and the mechanisms described by Kitchell et al. (1977). In general, *P* values of 0.5 or greater are required to accomplish sizes of 22.7 kg or more within a 10-yr period of life in the lake. We estimate that few fish will survive beyond 10 yr after stocking. At high feeding rates ($P = 0.9$), salmon can reach 22.7-kg weights in 3–4 yr and 45-kg weights in 4–5 yr.

Modeling Observed Growth

The observed standard chinook growth rates and extrapolated sterile chinook growth rates result in estimates of *P* values from 0.49 to 0.80 (Tables 1 and 2). Growth efficiencies peak at greater than 30% and decline to 10% for older, sterile salmon.

Based on the proportions of prey types in the diet reported by Stewart et al. (1981), we calculated the daily feeding rates of both sterile and standard chinook. Daily feeding rates for standard chinook salmon (maturing at the three different rates) exhibit both temperature and size effects with peak predation rates occurring in late summer when individual fish are at a large size and temperatures are high (Fig. 3). Although a mixture of prey types is eaten during the first year in the lake, adult alewife become the dominant component of the diet in the second and all subsequent years (Stewart et al. 1981; Hagar 1984).

TABLE 3. Cumulative consumption (kg) of individual chinook salmon partitioned by prey type. Standard fish are compared with sterile fish reaching 22.7 kg (50 lb), 45.4 kg (100 lb), or surviving 10 yr in the lake. Consumption equivalents are the number of standard life history fish that would consume the same amount of prey as an individual sterile fish.

Chinook group	Invertebrates	YOY alewife	Adult alewife	Other fish	Total consumption	Consumption equivalent
Standard (9 kg)	0.05	1.43	39.4	2.85	43.8	1.0
22.7 kg	0.05	2.34	95.5	6.06	104.3	2.4
45.4 kg	0.05	5.34	282.5	16.67	304.6	7.0
10 yr	0.05	8.01	448.6	26.12	482.7	11.0

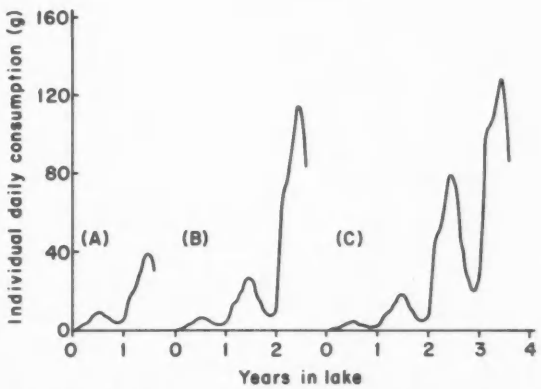

FIG. 3. Individual daily consumption for chinook salmon representing the standard patterns of growth.

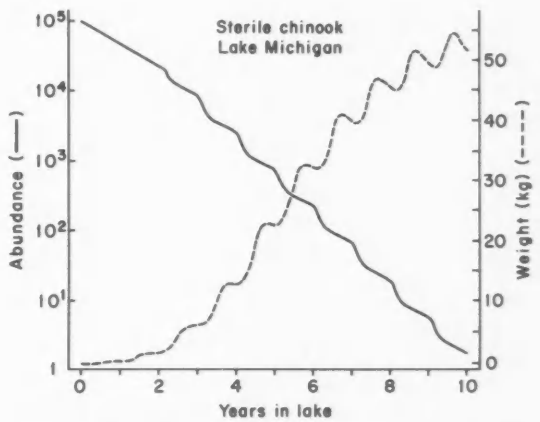

FIG. 4. Extrapolation of current growth rates and mortalities (Stewart et al. 1981) to sterile chinook salmon in Lake Michigan.

Our extrapolation to the extended life span of sterilized chinook is based solely on the feeding and growth pattern of the 4-yr maturing, standard chinook. Sterile salmon may reach 22.7 kg (50 lb) early in the sixth year in the lake and 45.4 kg (100 lb) after 8.3 yr in the lake (Fig. 4). Abundance estimates (Fig. 4) include natural mortality rates estimated from standard fish and fishing mortalities modified from estimates of catch rates on standard fish in ways we will describe later. A cohort of 10^5 sterile chinook has a functional estimated life span of a decade.

Estimates of Total Predation

Cumulative consumptin for an individual fish surviving to the end of the standard life span (spawning in year 4) is much less than that of a sterile fish reaching 22.7 or 45.4 kg (50 or 100 lb) (Table 3). The relative impact on the forage base for a sterile fish surviving to these weights are up to 11 times greater than a 4-yr-old standard chinook. The high consumption amounts are much greater than the relative weights of the fish being compared and demonstrate the importance of age as a factor affecting cumulative consumption. A 45.4-kg sterile chinook will consume 7 times the prey consumed by a 4-yr-old standard chinook, and yet weigh 5 times the weight of the standard fish (Table 3).

Our primary goal was to estimate the total demand on forage resources by a cohort of sterile salmon. Toward that end, we calculated the daily consumption rates for a cohort of 10^5 sterile chinook salmon with growth and survival rates as depicted in the preceding section and Fig. 4. The results of that calculation (Fig. 5) show daily consumption rates for a 10-yr period. Peak demand on prey resources occurs 3–4 yr after stocking of a sterile cohort. Stewart et al. (1981) termed the lag between time of stocking and peak forage use as "predatory inertia." As the lag period of a predatory inertia effect increases, changes in stocking rate cease to become a viable management tool for managing the predator–prey system. Stocking sterile salmon increases the lag period beyong the 2- to 3-yr lag previously estimated for chinook (Stewart et al. 1981).

Total lifetime consumption for a cohort (10^5 fish) of sterile chinook salmon is 40% greater than for the same cohort of standard chinook salmon across all prey types (Table 4). The total cohort consumption of adult alewife is 60% greater for sterile versus standard chinook salmon. These ratios suggest that stocking sterile fish will have roughly 1.4 times the effect on the forage species as stocking the same number of standard fish (Table 4). These calculations assume that large, sterile fish have the same diet as the standard fourth-year adults. It is reasonable to assume that the diets and distribution of larger fish will be different from those of the standard adult, but we have no basis for expectation. Among the possible prey that might become available to the sterile fish as they get larger are younger salmonines. We have not modeled the results of a shift in diet to include other salmonines, although it is highly likely that such a shift would have an impact on salmon survival rates and fishing return rates.

TABLE 4. Cumulative consumption (metric tons) by a cohort of 10^5 salmon partitioned by prey types. Standard and sterile chinook salmon are compared as in Table 3. Consumption equivalents are the number of standard life history fish that would consume the same amount of prey as the average sterile fish.

Chinook group	Invertebrates	YOY alewife	Adult alewife	Other fish	Total consumption	Consumption equivalent
Standard (9 kg)	5.15	65.1	363.4	61.1	494.7	1.0
22.7 kg	4.46	55.0	526.1	61.5	647.0	1.3
45.4 kg	4.46	55.6	564.3	63.6	688.0	1.4
10 yr	4.46	55.6	565.8	63.7	689.6	1.4

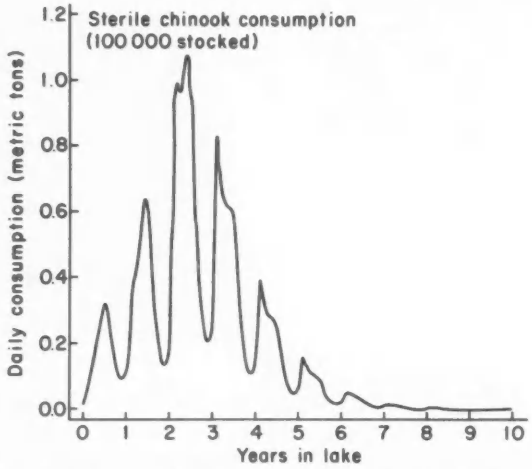

FIG. 5. Daily consumption for a cohort of 10^5 sterile chinook salmon.

TABLE 5. Predicted sport catch for cohorts of 10^5 sterile and standard chinook salmon stocked in Lake Michigan. Catches are categorized by year after stocking.

Year	Standard	Sterile
1	0	0
2	1 471	664
3	3 868	4070
4	4 661	3242
5	0	958
6	0	283
7	0	84
8	0	25
9	0	7
10	0	2
Total	10 000	9335
No. > 22.7 kg	0	308
No. > 45.4 kg	0	3

Yield to the Fishery

As stated in the section on the model, we estimated fishing mortality rates based on monthly catch statistics for Wisconsin waters of Lake Michigan (Bleser and Hansen 1985a, 1985b, 1985c). We subtracted the spawning run fisheries from the total catch to estimate the fishing mortality pattern for sterile salmon. Given a total return rate of 10% for standard chinook (Wisconsin Department of Natural Resources 1986), subtracting the spawning run fisheries results in a return of 8% for nonspawning fish (of the standard life span chinook). We calculated monthly fishing mortalities for standard fish that would fit the monthly catch distribution and result in a 10% total return. We assumed monthly mortalities to be constant across age classes susceptible to the sport fishery. As a check, the mean weight of the sport catch within the standard simulation was calculated to be 4.68 kg. Hansen (1986) reported the mean weight of chinook salmon caught from Wisconsin waters of Lake Michigan to be 4.73 kg (±1.0 kg). Our estimated fishing mortalities for standard chinook appear to fit the available data from Lake Michigan both in terms of size of fish caught and monthly distribution of catch.

For sterile chinook, we calculated monthly fishing mortalities for sterile salmon that would result in the predicted monthly catch totals and scaled those mortalities to give a total return of 8% for the first 4 yr of life of the sterile salmon (to fit the nonspawning return rate of 8% for standard fish). These mortality rates were then extended for the longer life span of sterile fish, resulting in a final return of 9.3%. The total predicted return to the sport fishery of sterile salmon is essentially the same as that of standard fish, with the increase in time exposed to the fishery offset by the increased susceptibility of standard fish during spawning runs.

Total sport catch for both standard and sterile chinook salmon peaks during the third and fourth years of life (Table 5). Sterile salmon 5 yr and older make up 14% of the total sterile salmon caught. The total return to the fishery of trophy size fish (those greater than 22.7 kg) is predicted to be 0.3%. The total biomass of salmon caught is slightly higher for sterile chinook (56 metric tons) versus standard chinook (47 metric tons) given the larger mean size of the sterile fish. Sterile chinook salmon stocked in 1986 will grow to trophy sizes by 1991 and may still appear in catches as late as 1996.

In conducting this analysis, we have made several important assumptions regarding the ecology and growth of sterile salmon. Will sterile salmon change prey preferences with size? If prey preferences change and their distribution differs from that now familiar to salmon anglers, will catchabilities change to the extent that lower mortalities might increase total demand on forage resources? Will these large predators switch to other, smaller salmonines, including juvenile lake trout, or adult *Coregonus* spp.? What are the socioeconomic values of a trophy salmon fishery to the Great Lakes fishermen and communities? There are many more questions and a substantial research

program should accompany the introduction of this new predator to the Great Lakes.

Conclusions

An energetics modeling analysis of sterile chinook salmon in Lake Michigan suggests certain considerations with regard to development of a trophy fishery:

(1) The total impact of sterile fish on forage species is approximately 50% greater than that of the same number of standard fish stocked. A stocking program including sterile fish should take into account the higher impact and the timing of that impact in formulating policies for the total stocking program.

(2) A cohort of sterile salmon may yield a slightly lower total return to the fishery. Certainly the yield will not increase in proportion to the high impact of sterile fish on the forage base. Given a finite resource, stocking sterile fish implies stocking fewer standard fish over each of several years, also having the effect of lowering yield. That cost must be weighed against the socioeconomic value of a new trophy fishery.

(3) There is the possibility that large sterile salmon will prey upon other valuable species (*Coregonus* spp. and/or smaller salmonines). An unknown ecological risk exists in that the configuration of current food webs may be substantially altered by the addition of predators that attain large size during their extended life span.

(4) Although a trophy fishery is likely to develop, the concentrations of contaminants in these large fish will probably make them unsuitable for human consumption. Agencies must accept the responsibility for informing the public of this potential hazard.

While we have raised several concerns about the stocking of sterile salmon, many benefits are also possible. A new trophy fishery can sustain and heighten public interest and continue to expand awareness of the values and constraints of Great Lakes fisheries operating in the larger context of whole ecosystems. The ecological consequences of these new predators and their economic contribution to the sport fishing industry remain open to incisive investigations. Unlike many of the surprises and calamitous changes that have occurred in the history of Great Lakes fisheries, there is ample time to plan and conduct effective research. Sterilized salmon stocked in 1986 will first appear in sport catches in 1988. Our assumptions about their growth rates, diets, and contributions to the fishery can be first tested then. By 1991 the first of the trophy fish should begin to appear in the fishery. We have time to prepare the appropriate questions and plan ways to get the desired answers.

Acknowledgments

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Prey Fish Dynamics and Salmonine Predator Growth in Lake Ontario, 1978–84[1]

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O'Gorman , R., R. A. Bergstedt, and T. H. Eckert. 1987. Prey fish dynamics and salmonine predator growth in Lake Ontario, 1978–84. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 390–403.

The size of hatchery-reared brown trout (*Salmo trutta*) and coho salmon (*Oncorhynchus kisutch*), 1 yr after release in Lake Ontario, declined when the stocking of salmonines was increased between 1978 and 1984. The principal prey species, alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*), failed to show the expected, predator-induced downturn in abundance. Instead, rainbow smelt remained moderately abundant and alewives very abundant. During this period, alewife year-classes were small, survival of yearling alewives was poor, growth of young-of-the-year of both alewives and rainbow smelt was slow (growth of most older alewives ceased), and rainbow smelt numbers gradually increased (the much larger alewife population presumably buffered older rainbow smelt from predation by large piscivores). When adult alewife numbers were halved by a winter die-off, the subsequent year-class of alewives was large and growth of brown trout during their first year in the lake increased. This suggested a causal relation between abundance of young alewives and brown trout growth. In the first year coho salmon were at liberty, their growth was related to abundance of young-of-the-year alewives; in their second year it was related to the abundance of yearling alewives and the condition of adult alewives. We hypothesize that abundant adult alewives suppressed production of young-of-the-year fish (necessary prey for salmonines during their first year in the lake) through competition for limited zooplankton production, and thus impeded the transfer of energy from the lowest trophic level to young salmonine predators.

La taille des truites brunes (*Salmo trutta*) et des saumons cohos (*Oncorhynchus kisutch*) d'élevage dans le lac Ontario, un an après leur mise à l'eau, a décliné suite à l'augmentation de l'ensemencement en salmonidés de 1978 à 1984. Les principales espèces-proies, le gaspareau (*Alosa pseudoharengus*) et l'éperlan arc-en-ciel (*Osmerus mordax*), ne sont pas devenues moins nombreuses à cause de l'action des prédateurs, comme cela avait été prévu. Au contraire, l'éperlan arc-en-ciel est demeuré relativement abondant et le gaspareau est devenu très abondant. Au cours de cette période, les classes annuelles du gaspareau étaient petites, la survie des poissons de l'année était faible, la croissance des jeunes de l'année du gaspareau et de l'éperlan arc-en-ciel était peu élevée (la croissance de la plupart des gaspareaux plus âgés a stagné) et le nombre d'éperlans arc-en-ciel a graduellement augmenté (la population beaucoup plus grande de gaspareaux ayant probablement servi de tampon et protégé les éperlans arc-en-ciel plus âgés de la prédation par les gros piscivores). Lorsque le nombre de gaspareaux adultes a diminué de moitié à cause d'une hécatombe d'hiver, ses classes annuelles subséquentes ont été importantes et la croissance des truites brunes, au cours de leur première année dans le lac, a augmenté. Cela porte à croire à l'existence d'une relation de causalité entre l'abondance des jeunes gaspareaux et la croissance des truites brunes. Au cours de la première année où les saumons cohos ont été relâchés, leur croissance a été en rapport avec l'abondanoe des jeunes gaspareaux de l'année. Au cours de la deuxième année, la croissance a été fonction de l'abondance des gaspareaux de l'année et de l'état des gaspareaux adultes. Les auteurs formulent l'hypothèse que la présence d'un nombre abondant de gaspareaux adultes a eu pour effet de supprimer la production de jeunes poissons de l'année (proies nécessaires aux salmonidés au cours de leur première année dans le lac) de par la compétition pour une production zooplanctonique limitée, et a donc limité le transfert d'énergie entre le niveau trophique le moins élevé et les jeunes salmonidés prédateurs.

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The open-water fish community of Lake Ontario is the least diverse of any in the Great Lakes. It is dominated by three species (Christie and Thomas 1981): alewife (*Alosa pseudoharengus*), the most abundant; rainbow smelt (*Osmerus mordax*); and slimy sculpin (*Cottus cognatus*). After extirpation of the native lake trout (*Salvelinus namaycush*) and virtual extirpation of burbot (*Lota lota*) in the 1950's (Christie 1973), offshore waters were almost devoid of large piscivores until the early 1970's, when massive annual stockings of hatchery-reared salmonines began. The principal species released were lake trout, chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), brown trout (*Salmo trutta*), and rainbow trout (*S. gairdneri*). From an initial planting of 76 000 fish in 1968, the number stocked annually rose irregularly to about 2.8 million in 1974 (Fig. 1). Releases did not exceed 3 million until 1980–81, when plantings increased sharply to about 4.5 million and then increased each year thereafter, exceeding 8 million in 1984.

Growth of predators is usually regulated by the abundance of their prey and, so we expected that when the numbers of salmonines being released began to reduce prey stocks, growth of predators would slow. In spring 1982, immediately after a substantial increase in the stocking rate, the size of brown trout and coho salmon declined markedly (Fig. 2, 3). This was alarming for two reasons: (1) recent hatchery construction insured that future stocking rates would far exceed the 1982 rates that had seemingly depressed growth, and possibly survival; and (2) if the existing three-species combination of prey were destroyed, there were no other species of fish in the main lake capable of increasing in abundance sufficiently to compensate for the loss. The principal species that originally occupied the main lake (deepwater sculpin, *Myoxocephalus thompsoni*, and deepwater ciscoes, *Coregonus* spp.) were extirpated (Oswego Biological Station, unpubl. data; Crossman and Van Meter 1979). Therefore, a return to the historic, multispecies complex would be possible only if the deepwater sculpin and deepwater ciscoes were reintroduced from elsewhere.

We here review changes in numbers, growth, and recruitment of alewives and rainbow smelt during 1978–84; we offer hypotheses as to why the changes occurred; and we demonstrate how those changes affected the growth of brown trout and coho salmon. We also discuss the implications for management of our conclusion that reduced size of age II brown trout and coho salmon did not result from a reduction of prey density by hatchery-reared predators but rather from a hyperabundance of mature alewives.

Prey Assessment

Bottom trawls were used by the U.S. Fish and Wildlife Service (FWS) and New York Department of Environmental Conservation (NYDEC) to assess alewives and rainbow smelt. The 12-m (headrope) trawls had cod ends constructed of 9-mm-mesh (stretched measure) knotless nylon. Two bottom trawl surveys were conducted each year during 1978–85, one in late April to early May to assess alewives and the other in early June to assess rainbow smelt. Survey methodology was described by O'Gorman and Schneider (1986) and is reviewed only briefly here. We attempted to trawl at 10-m depth intervals through the range of depths occupied by the target species at 12 transects spaced roughly 25 km apart along the U.S. shoreline (Fig. 4; Table 1). A standard tow was made along the contour at 4.6 $km \cdot h^{-1}$ for 10 min and theoretically swept 0.5 ha of bottom.

To estimate the magnitude of the populations available to our gear (near bottom) in U.S. (New York) waters, we first divided U.S. waters into strata (seven for alewives and six for rainbow smelt). Stratification was appropriate because of large, consistent differences between catches at different depths or in different regions of the lake. Then we assumed that our catches constituted a stratified random sample and calculated the stratified mean catch per 0.5 ha and the 90% confidence intervals accordingly. Finally, these values were multiplied by the number of 0.5 ha's in U.S. waters to obtain the population estimate.

Age composition was determined by applying age–length keys constructed from aged samples of 500–600 fish of each species to much larger samples. Ages were determined from scales during 1978–83; thereafter, alewives were aged from otoliths and rainbow smelt from sections of pectoral fin rays. For alewives the change was prompted by the observation that otoliths yielded more accurate (older) ages (O'Gorman et al. 1987); for rainbow smelt, decreasing growth rates and the loss of scales by most small rainbow smelt caught in trawls necessitated the change to fin rays.

Mean lengths at age were calculated from the observed age–length distribution, except for rainbow smelt in 1977 when they were obtained by back-calculation from scale samples taken in 1978. Mean weights were derived from each year's age–length distribution and length–weight regression. Because rainbow smelt gonads were in a regressed state in June and sex determination was difficult, all analyses were made for sexes combined. Because of the relatively short data series and the desire to avoid too many type II errors, we accepted a significance level of $P \leq 0.10$.

Predator Assessment

Lengths and weights of brown trout and coho salmon were monitored by NYDEC in April and May by gill netting (1974–81 and 1983) and by sampling anglers' catches (1979–85). Gill nets were made up of equal-length panels of 10.2-, 12.7-, and 15.2-cm-mesh (stretched measure) netting. The nets were set, usually overnight, perpendicular to shore; the inshore end was as close to shore as possible, but not in water less than 2 m deep (generally it was 15–60 m from shore). Locations sampled and fishing effort varied between years Usually, nets were set at numerous sites in New York waters between the mouth of the Niagara River and Southwick, although in some years, nets were fished only between Hamlin and Fair Haven (Fig. 4). Sampling time within the April–May period also varied, and unlike the other changes, this difference affected the growth data (Cape Vincent Fisheries Research Station, unpubl. data): brown trout and coho salmon were significantly larger (t-tests, $P < 0.05$) in late May than in April. Growth in spring generally did not begin until after the first week of May but varied from year to year, apparently in response to differences among years in timing of spring water temperature increases. To avoid this potential bias, we did not use data collected in late May. Furthermore, because statistically significant (analysis of variance, $P < 0.05$) changes in weight occurred before those in length (Cape Vincent Fisheries Research Station, unpubl. data), we used total length to characterize size of predators in spring.

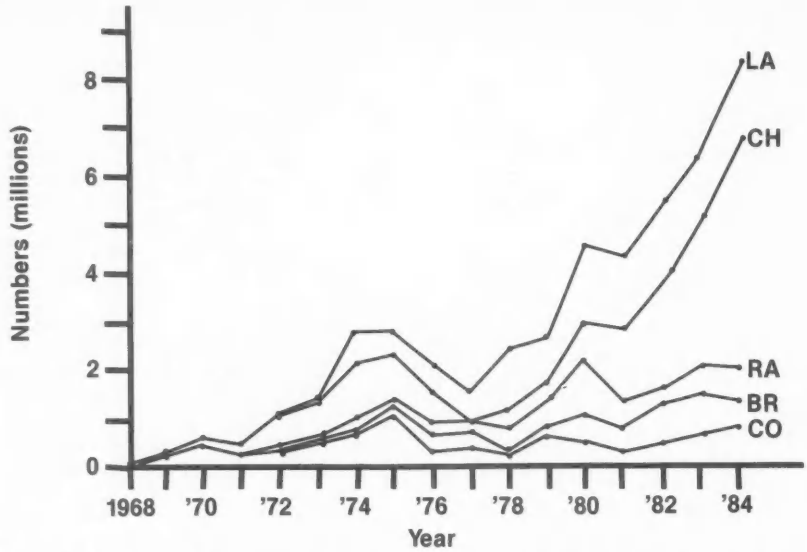

FIG. 1. Total numbers of hatchery-reared lake trout (LA), chinook salmon (CH), rainbow trout (RA), brown trout (BR), and coho salmon (CO) released in Lake Ontario, 1968–84. Data from Lake Ontario Fisheries Assessment Unit, OMNR, Richmond Hill, Ontario, and Cape Vincent Fisheries Research Station, NYDEC, Cape Vincent, New York.

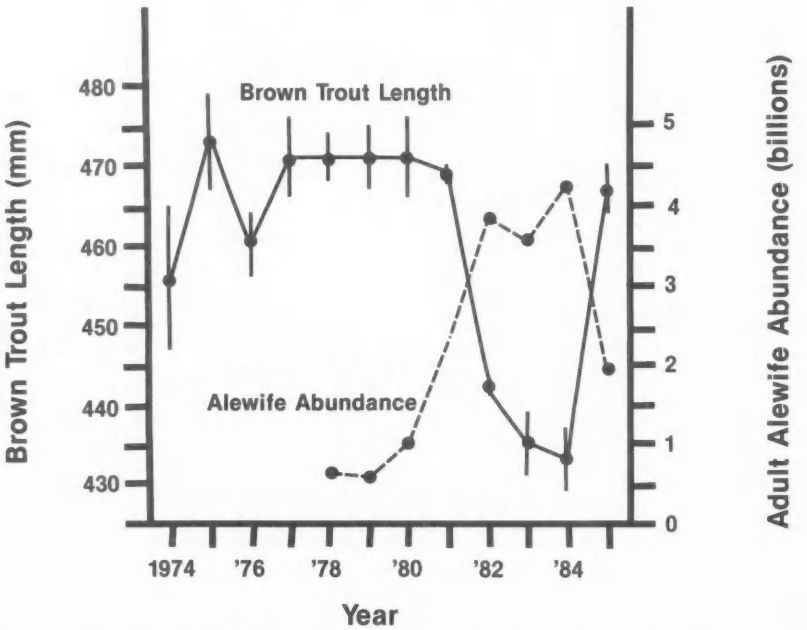

FIG. 2. Mean total lengths of age II brown trout in spring 1974–85 and the abundance of adult alewives (≥age II) during the brown trout's first lake year, Lake Ontario. Vertical lines are 95% confidence intervals.

Anglers' catches were examined over a 4-d period during late April in conjunction with a lakewide fishing derby. Chances for prizes were awarded for each fish registered to encourage the entry of all fish creeled. We examined catches at nearly all of the seven to nine derby registration stations scattered along the U.S. shoreline. In years when we sampled both with gill nets and at the derby, comparisons of length and weight (t-test) and proportions of fin-clipped fish (chi-square analyses) in each sample indicated no statistically significant difference between the two types of samples within any particular species – age

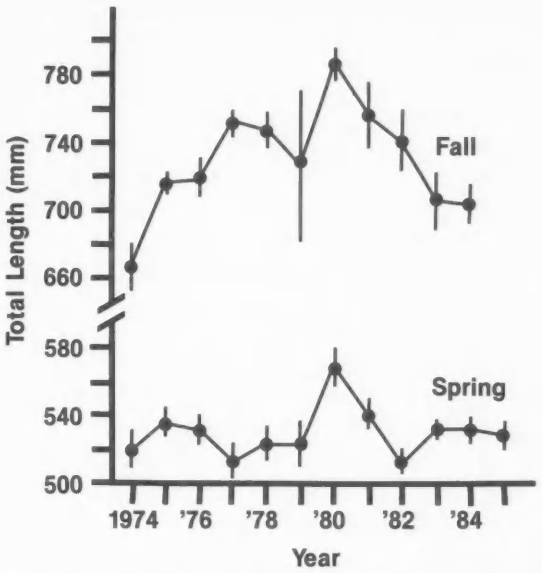

FIG. 3. Mean lengths of coho salmon at age II in spring and fall, Lake Ontario, 1974–85. Vertical lines are 95% confidence intervals.

group (Cape Vincent Fisheries Research Station, unpubl. data). We therefore combined data from both sampling methods for 1979–81 and 1983 and do not believe that the growth statistics were biased in years when only one sampling method was used.

The NYDEC also monitored size of mature, age II coho salmon in the fall by gill netting in the estuary of the Salmon River (Fig. 4). Gill nets consisting of equal-length panels of 10.2-, 12.7-, 15.2-, 17.8-, and 20.3-cm-mesh (stretched measure) netting were set overnight, parallel to the current. Fall netting was generally conducted once a week, from early September to mid-November.

In both spring and fall, all fish examined were measured (total length, millimetres), most were weighed (to the nearest 5 g in spring and 10 g in fall), and from some scale samples were removed. Scales were used to age all brown trout and coho salmon for which aging by length was questionable.

Predator Stocking

Brown Trout

Brown trout of different life stages as well as sizes were stocked in Lake Ontario during 1973–84 and the survival of these hatchery-reared fish depended on their life stage when released. Most brown trout were released as yearlings during April and May by NYDEC. Mean weights at stocking ranged from 61 to 113 g. Nearly all were from two brood stocks — the Catskill Hatchery and Rome Laboratory strains — maintained by NYDEC. In some years, large numbers of fingerlings were stocked in spring, summer, or fall. Most fingerlings were small fish, culled during production and released without differentiating marks. However, several groups of larger fall fingerlings (average weight 38 g) were given unique fin clips to compare their survival with that of yearlings. Survival of yearlings was eightfold higher than that of fingerlings (Cape Vincent Fisheries Research Station, unpubl. data).

TABLE 1. Number of transects fished and trawl tows made in the assessment of alewife and rainbow smelt populations in Lake Ontario, 1978–85.

	Alewife		Rainbow smelt	
Year	Transects	Trawl tows	Transects	Trawl tows
1978	6	49	11	90
1979	11	105	11	89
1980	12	118	11	107
1981	10	88	11	90
1982	12	112	11	87
1983	12	93	11	86
1984	12	107	11	79
1985	12	118	11	75

Releases of brown trout by the NYDEC were augmented by those of the Ontario Ministry of Natural Resources (OMNR) during 1981–84, accelerating the gradual buildup of a lakewide population. Of the brown trout planted in Lake Ontario, the OMNR released 2% in 1981, 6% in 1982, 15% in 1983, and 23% in 1984. Fingerlings were stocked in 1981–82 and yearlings in 1981–84. For our analysis, we assumed that all brown trout of age II and older that we captured originated from NYDEC releases of yearlings because (1) the proportion released by OMNR was small and they were released far from our sampling sites; and (2) the survival of fall fingerlings was always much lower than that of yearlings, and the survival of smaller fingerlings released in spring and summer was probably even poorer. Numbers of brown trout stocked each year followed the irregular upward trend in the overall numbers of salmonines stocked (Fig. 1). Releases of brown trout yearlings rose from 60 000 fish in 1973 to more than 218 000 in 1979, nearly 400 000 in 1981, and more than 500 000 in 1982. Although the survival of the planted fish probably varied from year to year, the population of brown trout in the lake was generally increasing throughout the study period.

Coho Salmon

Numbers of coho salmon stocked fluctuated without trend within a relatively narrow range during the study period. Both OMNR and NYDEC stocked the species during 1973–84, usually releasing between 300 000 and 600 000 fish, although the number exceeded 800 000 in 1975 and 1984 (Fig. 1). Natural reproduction also contributed fish to the population, but we believe the number was small because few tributaries were suitable for successful spawning.

In our analysis we used only data from coho salmon released as yearlings by NYDEC. This agency released most coho salmon as yearlings from late winter to late spring. Mean weight at stocking ranged from 22 to 38 g. The coho salmon originated from stocks in Alaska, Oregon, Lake Michigan, and eventually Lake Ontario. Although the differences in origin probably affected growth rates, we believe that the effect was small compared with that of prey availability.

All or a part of the coho salmon released by NYDEC or OMNR were marked with fin clips, except for fish of the 1979 year-class. Consequently, in all but one spring (1981), we were able to identify fish stocked by the NYDEC when fish from both agencies intermixed along the south shore. We estimated the length of age II NYDEC coho salmon in spring 1981 from the mean size of all age II fish, based on the historical ratio of each

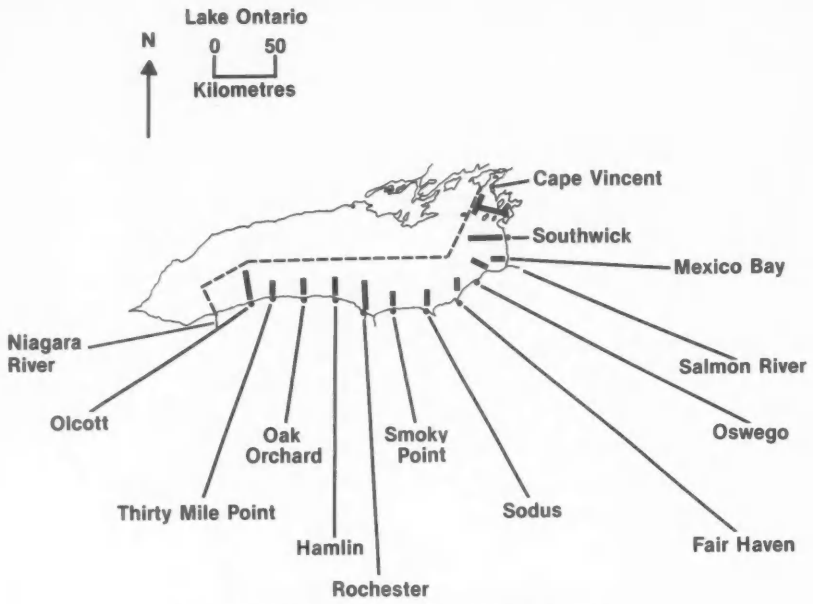

FIG. 4. Location of areas sampled with bottom trawls.

agency's fish in the catch and on average differences in their size. All fish caught in the Salmon River, New York, in fall were assumed to have originated from NYDEC plantings, even though some lacked identifying marks.

Prey Dynamics

Alewife

Size of the alewife population in Lake Ontario fluctuated widely during 1976–85 because of two weather-related die-offs. The stock collapsed during the winter of 1976–77 when unusually harsh weather triggered a severe die-off. The population then rose from low abundance to hyperabundance within 4 yr (1977–81). Abundance remained high through 1983 before another, albeit smaller, die-off in winter 1983–84 again sharply reduced the population (Table 2). On the basis of observations made during 1976–85, we describe here the relationship of population size to recruitment, survival, growth, and condition through a complete cycle of abundance: post-die-off, recovery, hyperabundance, and then another die-off. Although some of the changes that occurred in 1976–82 were described by O'Gorman and Schneider (1986), a synopsis is presented here for continuity.

The numbers of adult (age II and older) and yearling alewives available to our gear in U.S. waters in spring suggested a Ricker-type spawner-progeny relationship for alewives in Lake Ontario (Fig. 5). Small year-classes were produced in 1977–78 and in 1981–83, when the numbers of adults were low and high, respectively. The 1980 and 1984 year-classes, the most abundant at age I, were produced by an intermediate number of adults. Although trawling in spring 1977 was not sufficient to quantify adults, we estimated the number of spawning fish by applying the mortality rate of adults during 1978-81 to the 1978 catch of adults (no age II fish augmented adult numbers in 1978 because the 1976 year-class was missing, probably having been eliminated during the 1976–77 winter).

TABLE 2. Point estimates, ±90% confidence intervals, of the number and biomass of yearling and adult alewives near bottom in the U.S. waters of Lake Ontario during late April – early May, 1978–85. Also shown (in parentheses) is the percentage of the adult portion of the population that was of age II.

	Yearlings		Adults	
Year	Fish (millions)	Metric tons (thousands)	Fish (millions)	Metric tons (thousands)
1978	87±23	0.5±0.1	572±144 (0)	24.5±6.3 (0)
1979	98±51	0.8±0.4	1006±416 (67)	31.8±12.9 (50)
1980	552±397	4.1±3.2	2300±925 (19)	81.3±34.4 (12)
1981	1401±723	7.0±3.6	3850±1,071 (23)	121.5±34.5 (15)
1982	187±42	0.9±0.2	3545±1,350 (22)	110.9±43.4 (13)
1983	244±136	1.2±0.6	4236±1,551 (3)	135.0±50.3 (2)
1984	300±104	1.5±0.5	1966±576 (9)	59.6±17.4 (5)
1985	871±270	3.6±1.1	3739±772 (43)	84.1±16.2 (26)

Survival of alewives during their second year of life varied more than 10-fold, greatly modifying year-class strength before maturity. Survival in the second year of life declined markedly during 1978–81 as the population recovered from the 1976–77 die-off, remained low in 1982–83 when adults were abundant, and then increased sharply in 1984 after adult numbers were reduced by another winterkill. The $\log_{10}$ of survival in the second year of life (abundance at age II/abundance at age I) was negatively correlated with the number of adult alewives in April–May of that year ($r = -0.94$, $P < 0.01$; Fig. 6). The estimated number of fish in some year-classes was higher at age II than at age I, suggesting that catchability or availability was greater at age II. Nevertheless, the catch of yearlings was still an excellent measure of relative abundance at age I, and the ratio of

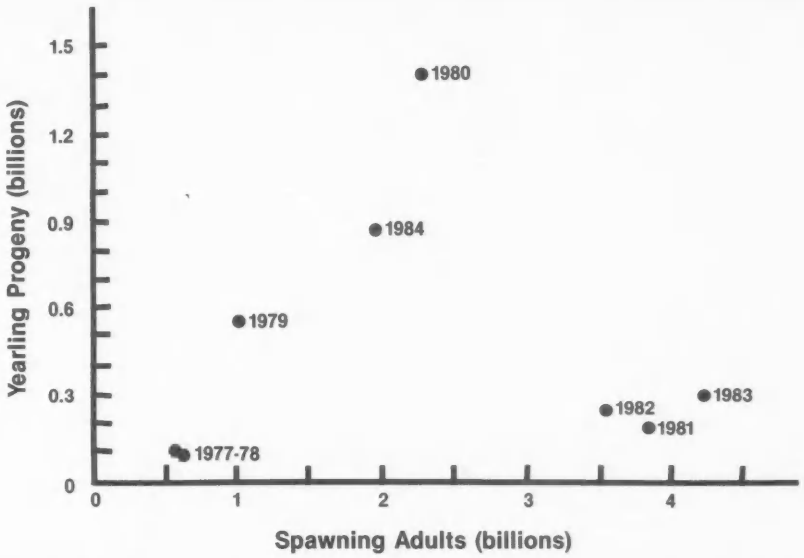

FIG. 5. Spawner–progeny relationship of alewives in Lake Ontario. Spawners are the number of adults (≥age II) near bottom in U.S. waters during spring 1977–84; progeny are the number of age I fish in the 1977–84 year-classes near bottom in U.S. waters.

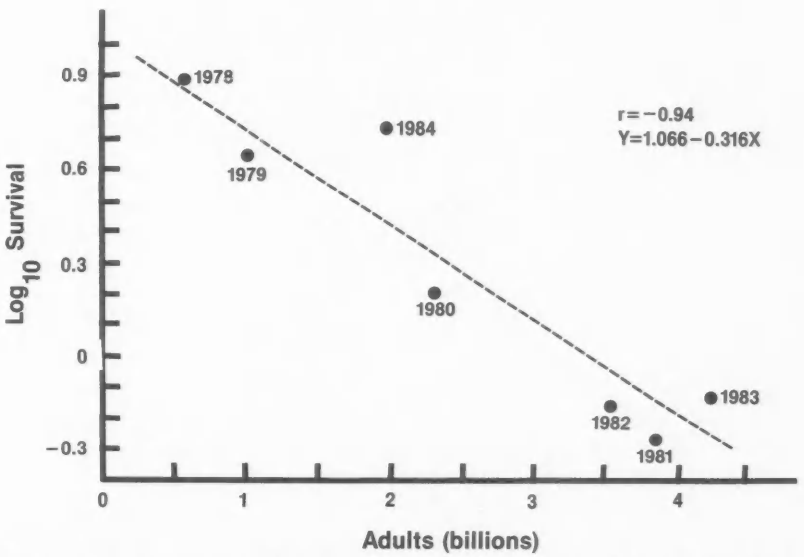

FIG. 6. Relationship of annual survival of alewives from age I to age II during 1978–84 to the abundance of adult alewives (indexed by the number of adults near bottom in U.S. waters) when each cohort was age I.

abundance at age II to that at age I was a reliable index of relative survival in the second year of life.

Adults probably controlled yearling survival through depletion of zooplankton during the spring stress period when the two life stages intermixed (bottom trawl catches contained both adults and yearlings from April through mid-June but mostly adults in mid-July; Oswego Biological Station, unpubl. data). The effects of an abundant alewife population on zooplankton — the elimination of larger forms and an overall decrease in density — have been well documented (Wells 1970; Vigerstad and Cobb 1978; Kohler and Ney 1981). In spring, when the density of crustacean zooplankton is beginning to increase from winter lows to a peak in August (Watson 1974; Borgmann et al. 1984), intense zooplanktivory could severely reduce zooplankton available for younger fish and thus depress survival. Furthermore, the small yearlings are apparently obligate planktivores whereas the larger adults are able to eat other food, such as zoobenthos (Morsell and Norden 1968).

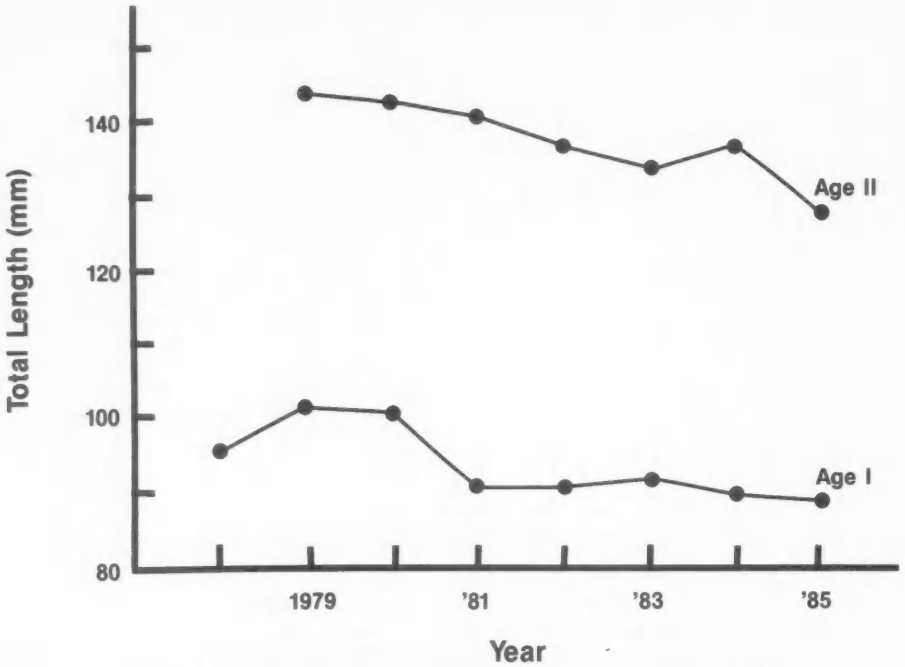

FIG. 7. Mean lengths of alewives of age I and age II in Lake Ontario, 1978–85.

Growth of young-of-the-year alewives was influenced by the size of the alewife population whereas that of yearlings was not, and this suggested that the distribution of yearlings during the growth period differed from that of other life stages. Growth in the first year of life declined after alewives became moderately abundant in 1980. Mean length of yearlings was 100 mm in 1978–80 but only 91 mm in 1981–85 (Fig. 7). However, growth increments in the second year of life were variable; no pattern of persistent decline was evident as the population expanded. Lengths of age II alewives averaged 143 mm in 1979–81, 136 mm in 1982–84, and 128 mm in 1985. The decline in mean lengths of the 2-yr-olds, 1 yr after that of the yearlings, suggests that the smaller 2-yr-olds in 1982–84 resulted from reduced growth during the first year of life. The further decline of size of the age II's in 1985 was probably the result of that cohort's extreme abundance (at age II, fish of the 1983 year-class were 2–12 times more abundant than the 2-yr-olds of any of the previous six year-classes). Yearlings seemingly do not inhabit the same region of the lake as that occupied by the older life stages during the growing period; if they did, competition for the finite zooplankton would surely have resulted in progressively smaller length increments in the second year of life during 1977–83. Also, the increment gained in 1984, after the adult population declined, would not have been the smallest observed. Indeed, catch data from a series of oblique midwater tows with a 3-m square net in August 1981 suggested that the yearlings are farther off shore during late summer. These tows, which we made at night over various bottom depths between shore and the 70-m bottom contour, yielded 601 alewives <70 mm long (young-of-the-year), 49 alewives >144 mm long (age II and older as judged by these lengths), but no fish 70–144 mm long.

The changes in growth of adult alewives during 1977–85 could not be described precisely because one of the techniques used to determine age was found to be unreliable. Scales were used to age alewives each year until 1984, when a comparison of ages determined from scales and otoliths indicated that scales are not a reliable structure for aging Great Lakes alewives after their second year of life, especially when abundance is high (O'Gorman et al. 1987). Consequently, ages based on scales became increasingly suspect as the population recovered, and could not be used to reliably identify older year-classes in successive years. Adults that survived the 1976–77 die-off, however, were readily identifiable because they grew so rapidly in 1977 that a wide, unmistakable growth zone was formed on their scales (O'Gorman and Schneider 1986). After 1977, growth of survivors slowed greatly and virtually ceased in 1980, before the population peak of 1981. Among the younger adults, the modal age group (as determined from scales) in scale–age frequencies did not advance from IV in spring 1981 to V in spring 1982, strongly suggesting that growth of all but the youngest adults ceased in 1981. In spring 1983 the modal scale–age group declined to III, suggesting that growth was ceasing at progressively younger ages and smaller sizes. Ages determined from scales and otoliths collected in fall 1983 indicated that in 1983, few adults increased in length after the fourth year of life and that many stopped growing after the third year of life (O'Gorman et al. 1987).

Precise definition of annual changes in survival of adult alewives was confounded by our inability to accurately identify year-classes from scales. Survival estimates for groups of year-classes (for example, the ratio of fish of age III and older in year $T + 1$ to fish of age II and older in year T) frequently exceeded 100%, the apparent result of a high survival rate

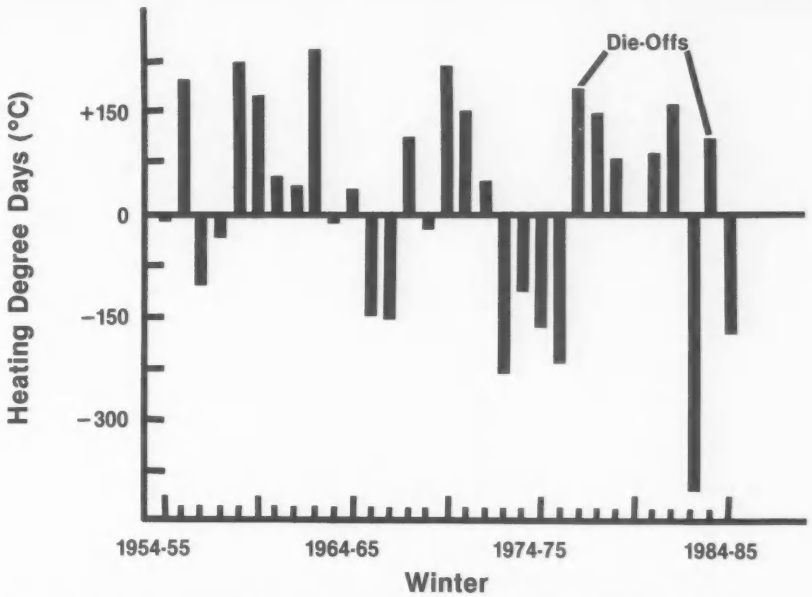

FIG. 8. Deviations from mean heating degree days (base 18.33°C, 1934–84) recorded each November 1 – March 31 winter season during 1954–85 by the National Weather Service at Rochester, New York (NOAA 1934–85). Positive deviations denote colder than average winters.

interacting with the sampling error inherent in measuring population size and assigning fish to age groups. For alewives with wide bands of growth on scales, survival apparently exceeded 95% while the population was recovering, but decreased to about 40% when alewives again became abundant. Of the survivors present in spring 1983, only 6% survived the 1983–84 stock reduction (otolith-age frequencies indicated that survivors aged VIII–XI made up 1% of the population in 1984). Survival of the younger adults from post-1976 year-classes did not decrease after the population rebuilt; estimates of their annual survival rate remained near 100% during 1981–83 but only 42% survived the 1983–84 winterkill.

Condition (K) of adult alewives in Lake Ontario varied inversely with population size. Condition increased sharply after the 1976–77 die-off and then gradually decreased as the population rebuilt. To index adult condition, we used the K-factor of 165-mm alewives, where $K = (10^5)(W) \div 165^3$ and W was the weight of a fish 165 mm long predicted from length-weight regressions. This index rose from 0.77 in fall 1976 to 0.91 in fall 1977 but had fallen to 0.72 by fall 1981 (Table 3). Condition always improved between spring and fall during 1978–82; average increase in K was 0.03. However, in 1983, the year in which adult numbers peaked (Table 2), the condition index in fall was 0.03 below that in spring. Loss of body weight by adults during the summer growing season suggests that the population exceeded the carrying capacity of the lake in 1983. This excess undoubtedly contributed to the severity of the mortality in the following winter. Even though the number of adults was substantially lower in spring 1984, condition improved only marginally by the fall, in sharp contrast with the large improvement in condition that followed the 1976–77 die-off. However, adults had to share food resources with yearlings in 1984 (1.6 billion age II fish were present in spring 1985 whereas none were present in 1978) and also with large numbers of young-of-the-year of both alewives (yearlings were 10 times more abundant in 1985 than in 1978) and rainbow smelt (the 1984 year-class was the strongest of the 1977–84 period).

TABLE 3. Indexed condition factor (K) of 165-mm alewives during spring and fall, Lake Ontario, 1976–85.

Year	Spring	Fall
1976	—	0.77
1977	—	0.91
1978	0.81	0.82
1979	0.78	0.82
1980	0.76	0.78
1981	0.69	0.72
1982	0.68	0.73
1983	0.69	0.66
1984	0.64	0.67
1985	0.62	0.67

Winter weather, not predation by stocked salmonines, was the principal factor influencing abundance of alewives in Lake Ontario during 1976–85. Alewife numbers were sharply reduced by die-offs during the winters of 1976–77 and 1983–84. Both winters were colder than average and were immediately preceded by a winter warmer than average (Fig. 8). We suspect that warm weather allows a greater proportion of the weaker individuals to overwinter. Inasmuch as alewife numbers were high in 1982, we hypothesize that it was the mild 1982–83 winter that enhanced survival and allowed the population to exceed the lake's carrying capacity in 1983. When climatic

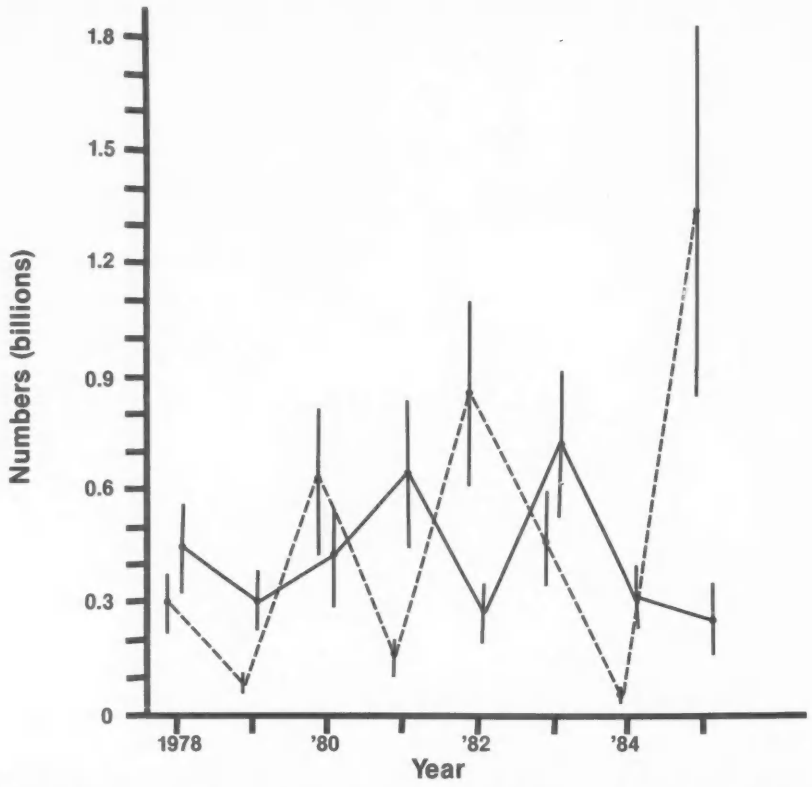

FIG. 9. Numbers of rainbow smelt yearlings (broken line) and adults (solid line) near bottom in U.S. waters of Lake Ontario during June 1978–85. Vertical lines are 90% confidence intervals.

conditions became severe in 1983–84, a die-off ensued. Also, warm winters would probably facilitate the recovery process; perhaps that is why Lake Ontario's alewives rebounded so rapidly after the 1983–84 die-off. On the other hand, colder weather does not allow the weaker individuals to overwinter. Elimination of the weakest fish in winter might reduce numbers sufficiently to offset the gain from recruitment the following year, inhibiting the population from recovering when numbers are low and keeping it below carrying capacity when numbers are high. Indeed, cold weather may have helped keep the alewife population below carrying capacity in 1982. Abundance declined between spring 1981 and spring 1982, and the intervening winter was the second coldest during the study period. In 1982 the condition of adults improved more over summer than in 1981 and was higher in fall (Table 3). This suggests that even with recruitment the total population in 1982 was smaller than in 1981.

Rainbow Smelt

The rainbow smelt population in Lake Ontario was smaller and considerably more stable than the alewife population (Fig. 9). Estimates of the biomass of rainbow smelt near bottom in U.S. waters during 1978–85 averaged 6516 t (coefficient of variation, 32%) whereas that of adult alewives alone averaged 81 089 t (50%). During the period of study, rainbow smelt growth declined, survival increased, and a regular pattern of recruitment became erratic. All of these changes appeared to be caused, either directly or indirectly, by the resurgence of the much larger alewife population.

Fluctuations in the abundance of yearlings indicated a pattern of alternating strong and weak year-classes. From 1978 to 1983, yearling abundance ranged from 1.8 to 7.4 times higher in even-numbered years than in adjacent odd-numbered years (Fig. 9). Because the adult portion of the population was largely of age II, adult catches generally followed the same alternating pattern. That pattern was broken in 1984 by a second consecutive low catch of yearlings. The two poor year-classes were then followed in 1985 by the strongest year-class observed as yearlings during 1978–85.

Although year-class strength varied greatly between adjacent years, there was also a pattern of increasing year-class strength. Through 1983, each successive group of yearlings in even or odd years was larger than in the previous even or odd year (Fig. 9).

Growth of rainbow smelt changed substantially, peaking during 1977 and generally declining through 1983 (Fig. 10). The initial change was most apparent among the younger fish, and the cumulative effects gradually reached the older age groups. Growth during both the first and second years of life was fastest in 1977; it was slowest during the first year of life in 1981 and during the second in 1983. Average size of fish in the first year of life was 85 mm (3.3 g) in 1977 compared with 66 mm (1.5 g) in 1981; growth increments for fish in the second

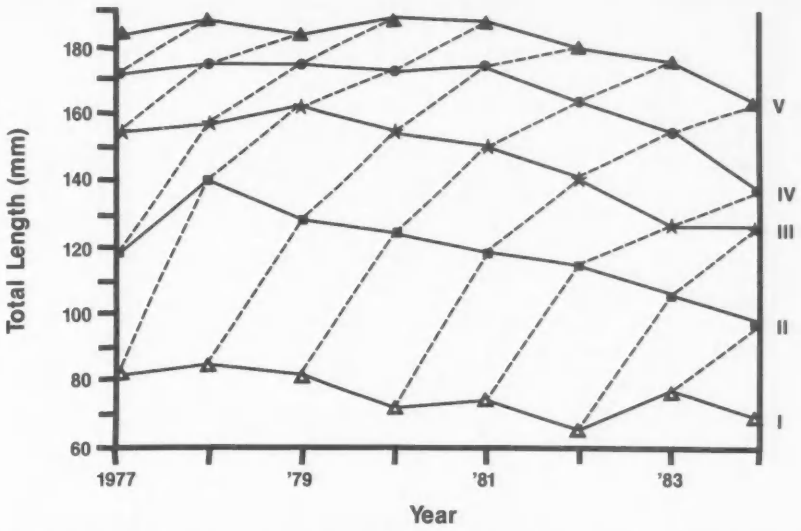

FIG. 10. Mean lengths of rainbow smelt at ages I–V in Lake Ontario during June 1977–84. Broken lines connect mean lengths of fish in a single year-class in successive years.

year of life were 59 mm (11.3 g) in 1977 and 21 mm (3.1 g) in 1983.

The decline in growth rate of rainbow smelt was directly related to the recovery of the alewife population from the 1976–77 die-off. The total length of age I rainbow smelt in June was significantly correlated ($r = -0.81$, $P < 0.05$) with the numbers of age I and older alewives in April during 1978–84. Correlations with length increments for years 2–6 were not significant (the range for r was -0.50 to -0.65). Young rainbow smelt are planktivores whereas older rainbow smelt feed mainly on benthic macroinvertebrates (Gordon 1961; Foltz and Norden 1977). The reduction of zooplankton by alewives probably caused the decline in growth of young rainbow smelt.

Fluctuations in length at age I (Fig. 10) also suggested that first-year growth of rainbow smelt was partly density dependent. Superimposed on the general decline in length at age I was a distinct pattern of alternating highs and lows. With the exceptions of 1978 and 1984, the highs corresponded to small year-classes and the lows to large year-classes. However, growth of rainbow smelt in the first year of life was not significantly correlated with their abundance at age I ($r = -0.43$, $P > 0.10$). Perhaps the relationship was real, but a longer data series would be needed to establish statistical significance.

The pattern of year-class strength at age I relative to the numbers and size of older fish present during the previous year suggested that the number of yearling (or small) rainbow smelt was the most important factor influencing survival of young-of-the-year. Regier et al. (1969) observed an alternating pattern of year-class strengths for rainbow smelt in Lake Erie and hypothesized that predation by yearlings on young-of-the-year (due to overlapping spatial distributions) was responsible for the 2-yr cycle. If size and not age determines the degree of spatial overlap between young-of-the-year and older fish, the break in the 2-yr cycle in Lake Ontario in 1984 may still be compatible with that hypothesis. The estimated mean length of age II rainbow smelt in June declined each year from 141 mm in 1978 to 98 mm in 1984, a length previously associated with yearlings. If a substantial part of the large 1981 year-class at age II had a spatial distribution similar to that of yearlings in 1983, predation by the combined 1981 and 1982 year-classes could have severely suppressed the 1983 year-class. In turn the small number of yearling and age II fish in 1984 could have resulted in the large 1984 year-class.

Potential egg deposition did not appear to be an important factor affecting year-class strength of rainbow smelt. The relatively small number of rainbow smelt of age II and older in 1984 produced the largest year-class of yearlings, despite the fact that mean lengths (as an indication of fecundity) in 1984 were the smallest observed at ages II–VI during June in 1978–85.

Because the growth of young rainbow smelt was influenced by alewife abundance, alewives may also have had an indirect effect on the year-class strength of rainbow smelt. If so, year-class strength would alternate on a 2-yr interval during periods of low alewife abundance, but the interval would increase during periods of high alewife abundance.

Fluctuations in the size of the alewife population also influenced the survival of older rainbow smelt. The average survival in the third to the fifth years of life (June to June) was significantly correlated ($r = 0.80$, $P = 0.06$) with the abundance of alewives in that year (Fig. 11). Survival of rainbow smelt was calculated by dividing the pooled abundance estimates of age groups III–V in year $T + 1$ by the pooled abundance of age groups II–IV in year T. Alewife abundance during a given year (June to June) was indexed by the estimated abundance of alewives of age I and older in April of year $T + 1$. High alewife abundance probably increased rainbow smelt survival; the number of rainbow smelt eaten by predators would be expected to decrease in years of high alewife density because the probability that a prey fish encountered by a predator was a rainbow smelt would be decreased.

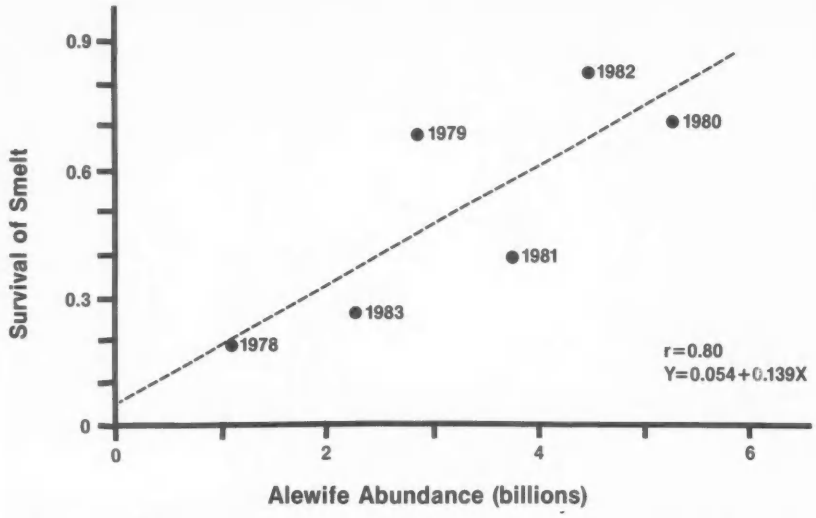

FIG. 11. Relationship of the survival rate of rainbow smelt from ages II–IV to ages III–V (June–June) to the numbers of alewives near bottom in U.S. waters in the spring (late April and early May) of the year the rainbow smelt were of age III–V, Lake Ontario, 1978–84.

Growth of Predators

Coho Salmon

Growth of yearling coho salmon (during their first year in the lake, here termed the first lake year) was not dependent on size at release, but appeared to be related to the biomass of young-of-the-year alewives available as prey. Mean lengths of age II coho salmon in spring 1974–85 ranged from 512 mm in 1982 to 569 mm in 1980; the overall mean was 530 mm (Fig. 3). Length in spring at age II was not correlated with mean weight at time of release (1974–85, $r = -0.01$, $P > 0.5$), but rather was significantly correlated (1977–85, $r = 0.65$, $P = 0.06$; Fig. 12) with yearling alewife biomass during that same spring. The biomass of yearling alewives was our best index of the biomass of young-of-the-year alewives available for prey of yearling coho salmon during the preceding summer. The small size of the prey was probably critical in permitting the change from an invertebrate to a fish diet and in permitting growth to a size at which the large adult alewives could be utilized.

The mean weight of coho salmon (age II) at their time of spawning in fall of their second lake year was influenced by the abundance of yearling alewives during the coho salmon's final growing season. The weight increment for coho salmon during the second lake year was not related to length at the start of the growing season ($r = -0.10$, $P < 0.5$). This lack of relationship suggests that their growth potential was so large that growth conditions in the second lake year mainly determined weight at spawning. There was a highly significant positive correlation ($r = -0.98$, $P < 0.001$) between weight of mature coho salmon in fall of 1977–82 and yearling alewife biomass during the preceding growing season (as indexed at age II the following spring; Fig. 13). Mean weights of mature coho salmon in fall 1983 and 1984, however, were much smaller than would have been predicted from the 1977–82 data. The correlation coefficient was reduced to 0.19 ($P > 0.5$) when the 1983 and 1984 weights were added. In view of the strength of the relationship over the first 6 yr, this reduction suggests that an additional factor began to influence growth during 1983–84. We speculate that the large change in condition of alewives (Table 3) may have influenced growth of salmon through changes in both lipid content and the nutritional value in the coho salmon's diet.

Brown Trout

At age II, brown trout in spring 1974–81 were unvaryingly large (Fig. 2). The overall, unweighted mean length and weight and their associated coefficients of variation were 468 mm (1.3%) and 1638 g (5.3%). In six of eight years the mean length fell within a 5-mm range and mean weight within a 100-g range. In 1982, however, a deviation from this pattern began. Brown trout were much smaller than in any previous year and their size declined still further in 1983 and 1984. Age II fish averaged 31 mm (7%) shorter and 444 g (27%) lighter in 1982–84 than in 1974–81. In 1985, however, brown trout were again large, with a mean size (467 mm and 1520 g) similar to that in the earlier period of fast growth.

Size of brown trout was less variable at age III than at age II. Mean lengths and weights and (in parentheses) coefficients of variation were 576 mm (1.2%) and 2883 g (5.4%) during 1977–85. Growth rates in the third year of life were accelerating in 1981–83 (years when the growth of younger brown trout was slowing); consequently, the size of age III fish did not decline substantially in 1982–84 (mean length was 574 mm compared with 576 mm in 1977–81). The greatest average length increment for the third year of life, 148 mm, was gained in 1984. Poor condition of adult alewives did not slow the growth of age II brown trout as it apparently did that of coho salmon, suggesting that nutritional requirements of the two species differed.

The size of brown trout at age II did not appear to be related to their weight when stocked as yearlings in spring. Substantial numbers of fingerlings were released in some years, but their survival was always much lower than that of yearlings;

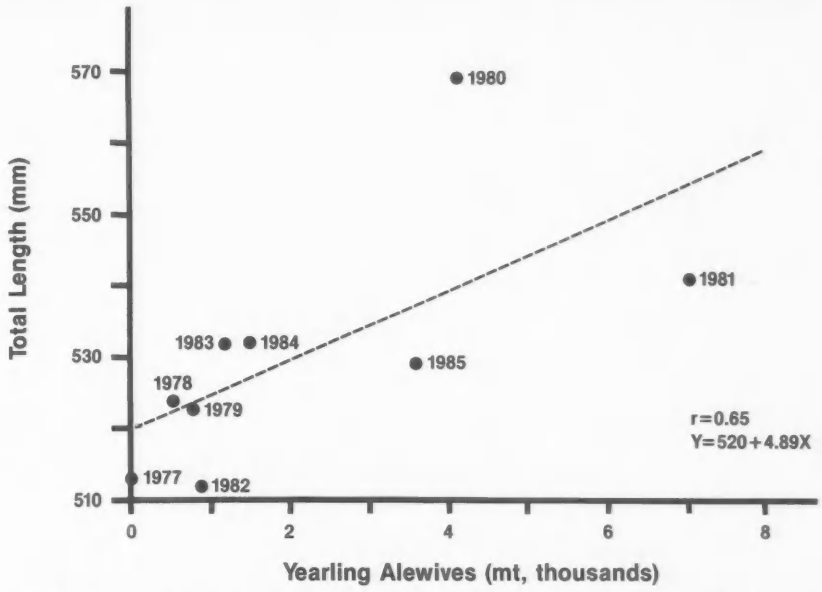

FIG. 12. Relationship of mean length of age II coho salmon in spring to the biomass of yearling alewives near bottom in U.S. waters the same spring (an index of the young-of-the-year alewives available for prey of age I cohos the preceding year), Lake Ontario, 1977–85. mt = metric tons.

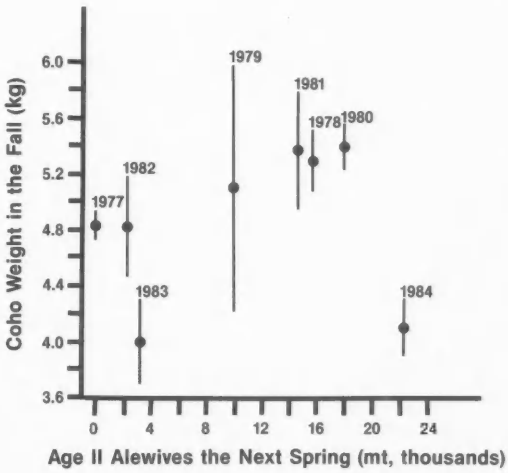

FIG. 13. Relationship of mean weight of mature age II coho salmon in fall to the biomass of age II alewives the following spring (an index of the yearling alewives available for prey of age II cohos), Lake Ontario, 1977–84. Vertical lines are 95% confidence intervals. mt = metric tons.

consequently, most age II fish were survivors of yearling plants. Although the smallest yearlings were stocked in 1979 and 1980 (average weight 61 and 69 g), these fish were among the largest at age II. Conversely, some of the largest yearlings were stocked in 1981 and 1983 (113 and 101 g) and they were among the smallest observed at age II.

Growth of brown trout during their first lake year declined precipitously when adult alewives were hyperabundant (1981–83), suggesting a causal relationship, particularly since rapid growth resumed when the numbers of adult alewives declined in 1984. When stocked, brown trout are too small to prey on adult alewives and thus must feed on the youngest alewives available, equally small fishes of other species, or invertebrates. We speculate that during 1981–83 the hyperabundant adult alewives usurped most of the planktonic secondary production, leaving little energy in the system for the elaboration of new fish biomass, particularly in young-of-the-year; thus the yearling brown trout lacked sufficient suitably sized prey to avoid a decline in growth. Indeed, the 1981–83 year-classes of alewives were not large and survival of yearlings in those years was poor. Although young-of-the-year rainbow smelt were abundant in 1981 and 1982, the brown trout apparently were unable to fully utilize them. Perhaps distributions of the two species did not overlap, or the thin, translucent rainbow smelt were difficult to see and catch. Difficulty of capture seems most likely, as we have rarely found rainbow smelt <70 mm long in the stomachs of salmonines. By age II, brown trout are able to eat adult alewives, and growth of the older brown trout remained rapid in 1981–83 when adult alewives were hyperabundant.

Discussion

For many members of the fish community in the open waters of Lake Ontario, growth, survival, and recruitment were largely determined by the dynamics of the alewife population (alewife dynamics were in turn influenced by winter weather). The mechanism by which alewives determined these processes appeared to be that of controlling zooplankton density, and perhaps also species composition. As alewife numbers increased, the reduced food supply led to (1) slower growth of young alewives and rainbow smelt (this slower growth eventually disrupted the feedback mechanism controlling the alterna-

ting cycle of strong and weak year-classes, i.e. predation by yearlings on young-of-the-year); (2) cessation of growth by many adult alewives; (3) decreased condition of alewives; and (4) decreasing survival of young alewives. Survival of older, nonplanktivorous rainbow smelt was enhanced as the increased numbers of alewives buffered them from predation. Among the predators, yearling brown trout and coho salmon depended on young-of-the-year of suitable size for rapid growth, and these were available in sufficient quantity only when alewives were not hyperabundant. Seemingly, by usurping most zooplankton production, the hyperabundant adult alewives suppressed production of young-of-the-year fish and thus impeded the transfer of energy from the lowest trophic level to young predators. Growth of age II brown trout remained rapid regardless of alewife numbers but that of age II coho salmon did not. Rather, salmon growth slowed sharply when hyperabundance depressed condition (K) of alewives below 0.70 (perhaps the lipid content or nutritional value of alewives had fallen below some threshold value).

If one knows the mechanism controlling alewife year-class strength and how alewife numbers and population structure affect predators and prey alike, is it possible to manipulate the forage population by judicious stocking of salmonines to ensure rapid growth of predators? Judging from the data we collected during 1977–85, salmonine production is clearly favored at intermediate levels of alewife abundance. While the data are admittedly not sufficient to manage for a quantitatively defined goal such as maximum sustained yield, maintenance of the alewife stock within a broad intermediate range of abundance index values would seem possible if predation were the main factor affecting mortality and recruitment.

Abiotic factors, however, may prevent successful management of a predator-prey system dependent on alewives. Sharp changes in alewife abundance caused by extremes of weather have been well documented (Brown 1972; Kohler and Ney 1981), and such changes are not only uncontrollable but also unpredictable. Improved condition of alewives at intermediate abundance levels will mitigate the severity of winter die-offs, but die-offs will probably continue to occur. Climatic conditions severe enough to cause catastrophic mortalities like that of 1976–77 have occurred five times during 1954–85 (Fig. 8). Although recovery of the alewife from the 1983–84 die-off in Lake Ontario was rapid, implying a high degree of resilience, the rapidity also suggests that preventing the population from expanding beyond a moderate level of abundance will require a larger standing stock of predators than was present in 1984. Furthermore, the rapid return to hyperabundance was entirely due to improved survival of yearlings. Response of the alewife population to a catastrophic die-off which eliminates the youngest cohort, as in 1976–77, under current or possibly even higher predator levels is uncertain. The predatory inertia of salmonines already in the lake (Stewart et al. 1981) might prevent any response by managers from stopping a population collapse. Possibly, a level of predation capable of reducing the standing stock of alewives would also be capable of preventing recovery from a major die-off. Such a scenario may have been followed in Lake Michigan: the beginning of the decline of the alewife there can be traced to a winter die-off in 1976–77 (Eck and Wells 1987).

If a climatic event triggers a major decline in the alewife stock, changes in the Lake Ontario fish community should be similar to those in Lake Michigan after the collapse of the alewife there: a resurgence of the yellow perch (*Perca flavescens*) and bloater (*Coregonus hoyi*) (Eck and Wells 1987). In nearshore Lake Ontario, not only would yellow perch rebound, but also white perch (*Roccus americanus*), a species not reported from Lake Michigan. Bloaters are absent in Lake Ontario (we caught only one during 1978–85), but lake herring (*Coregonus artedii*) maintain a remnant population. Thus the lake herring, in lieu of the bloater, might increase. Lake herring attain a much greater size than do alewives and would make suitable salmonine prey for only the first 2 yr of life. Rainbow smelt numbers would probably decline as predators switched prey, although total biomass, due to faster growth of individuals, would not change as rapidly. Predator growth would certainly decline, as would the survival of stocked fish. Given the dependence of the sport fishery on the rapid growth of hatchery-reared salmonines, the social costs of a decrease in the quality of the fishery due to declines in predator growth might be unacceptable. Considering such a cost, as well as the possibility of other, more deleterious changes (proliferation of some rare species such as burbot to "pest" levels or perhaps colonization by another exotic), a prudent course of management, and the one being adopted by the NYDEC (Eckert 1984), would be to ensure that the stock does not collapse.

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Vulnerability, Stability, and Coherence of the Fish Community in Lake Superior[1,2]

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Vulnerability analysis and spectrum analysis were found useful in examining potential structural changes in fisheries systems influenced by large perturbations. In the 1950's the Ontario fisheries of Lake Superior experienced a major perturbation due to invasion by sea lamprey (*Petromyzon marinus*). Vulnerability analysis indicated that invasion by sea lamprey and the consequent shifting of the fisheries to more intensive fishing on lower trophic level species resulted in higher vulnerability of the predatory fish species; i.e. likelihood of extinction increased. Spectrum analysis was then applied to the yield series of five fish species from Lake Superior. Analysis of the data before and after invasion by sea lamprey indicated major structural changes in the fishery: (1) except for lake trout (*Salvelinus namaycush*), either the dominant amplitude, the dominant frequency, or both decreased; (2) partial coherencies between pairs of yield series changed after the invasion; (3) lake whitefish (*Coregonus clupeaformis*) and lake trout replaced lake herring (*C. artedii*) as the species whose fluctuations in commercial yield were most highly synchronized with those of the other species of commercial importance.

Une analyse de la vulnérabilité et une analyse spectrale ont servi à l'examen des variations structurales potentielles de systèmes halieutiques faisant l'objet d'importantes perturbations. Au cours des années 1950, les pêcheries du lac Supérieur ont été fortement touchées par l'invasion de la lamproie marine (*Petromyzon marinus*). Une analyse de la vulnérabilité a indiqué que cette invasion et l'orientation subséquente de l'exploitation vers une pêche plus intensive des espèces appartenant à des niveaux trophiques inférieurs ont mené à une vulnérabilité plus élevée du prédateur, c'est-à-dire une plus forte possibilité de disparition. On a ensuite appliqué l'analyse spectrale à la série de rendements de cinq espèces de poissons du lac Supérieur. L'analyse des données recueillies avant et après l'invasion de la lamproie marine a indiqué d'importantes variations structurales de la pêche : 1) sauf pour le touladi (*Salvelinus namaycush*), l'amplitude ou la fréquence dominantes, ou les deux, ont baissé; 2) les cohérences partielles entre des paires de séries de rendement ont varié l'invasion; et 3) le grand corégone (*Coregonus clupeaformis*) et le touladi ont remplacé le cisco de lac (*C. artedii*) à titre d'espèces dont les fluctuations du rendement commercial coïncident le plus avec celles d'autres espèces à potentiel commercial.

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Much interest at the International Symposium on Stock Assessment and Yield Prediction (ASPY) revolved around the modeling and structure of fish communities (Christie et al. 1987; Colby et al. 1987; Evans and Loftus 1987; Evans and Waring 1987; Henderson and Fry 1987; O'Gorman et al. 1987). By structure we mean the qualitative and quantitative interspecific interactions which typify fish communities. These interactions are a reflection of the life history characteristics of the various species (e.g. feeding habits and habitat, timing of reproduction, density-dependent mechanisms, etc.) which may be viewed as adaptive strategies. The recent interest in harvesting multispecies fish communities (May et al. 1979; May 1984) further focuses attention on the need to analyze the structure of these communities.

It was realized at ASPY that structural changes may be reflected by decreases or increases in commercial yield, changes in species composition due to invasions or extinctions, changes in stability of the fishery, and changes in vulnerability of species to extinction. Some participants, admitting directionality in evolution, argued that due to coevolution, pristine fish communities are expected to be more productive than perturbed communities (i.e. coevolution results in communities which utilize resources more efficiently). Recent theoretical work suggests that evolution is not necessarily directional (Levins and Lewontin 1985). Even if it were, the theory of evolutionary stable strategies (Maynard Smith 1982; Vincent and Brown 1984) suggests that coevolution does not always result in more

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efficient use of resources by a coevolving community. At least in the ecological time scale, coevolution should result in structurally stable communities. However, after large perturbation to a structurally stable fish community (e.g. invasion by a new species, pollution), some change in a measure of community structure should be detectable. The intuitive realization of this fact has led to the wide discussion of "harmonic" communities (Ryder and Kerr 1978; Ryder et al. 1981).

The purpose of our paper is to demonstrate, by way of an example from the Canadian fishery in Lake Superior, the usefulness of two methods for analyzing structural changes in fisheries following perturbations. The first method, vulnerability analysis, was developed by Goh (1975), Grantham and Vincent (1975), Grantham (1981), and Vincent (1981). Given a mathematical model, it characterizes the set of all population densities possible for a community of coexisting biological entities (e.g. species) under partially unknown disturbances. One only needs to estimate the maximum possible disturbance to determine this set. Vulnerability analysis investigates how the set of all possible densities contracts or expands as a community is subjected to various magnitudes of perturbations. If the analysis reveals that one or more of the species' densities may exist at low densities, then the perturbations may cause extinction.

The second method, spectrum analysis, is widely used (Priestly 1981), but has not been applied to analysis of fish communities in the Great Lakes. We developed a method for quantifying the coherence of a fish community (i.e. the amount of coupling among the time series, of a relevant variable, of the component species in a community) and identifying important species, i.e. species whose fluctuations (in abundance, commercial yield, or other relevant measure) are synchronized with fluctuations of the rest of the community more than other members of the community. We label these as keystone species. Furthermore, suggestions are made which clarify the intuitive rather than the more rigorous theoretical (Pimm 1984) understanding of stability.

The two methods are different in approach. Vulnerability analysis is based on a deterministic model of the system and uses uncertain inputs to analyze changes in the community. Spectrum analysis is statistically oriented and relies on extensive data analysis. Yet, both methods have a single purpose: to improve our ability to detect structural changes in the fishery due to perturbations, and thus aid in management decisions. The methods are complementary in the sense that they provide different information on a fishery subjected to perturbations.

Vulnerability Analysis

Introduction

Vulnerability analysis is discussed in some detail by Vincent (1987) and Cohen (1987). Briefly, it can be outlined as follows. Suppose that a two-species model (by species we mean two functional groups, such as predatory species and prey species) has a stable equilibrium point. The populations at equilibrium are assumed to be perturbed by an external input. We know nothing about the input, except that it is bounded. It can be constant, it can vary with time, or it can be random. The purpose of the analysis is to determine the set of all possible states (where states are defined, for example, as species densities) to which the system can be driven by all possible inputs. This set, known as the reachable or vulnerability set, indicates how species population densities may change due to partially unknown disturbances. The relationship of the reachable set to undesirable states gives a measure of the vulnerability of the system. For example, if the vulnerability set indicates that one of the component species can be at or close to zero density under a given perturbation (whose bounds only are known), then the system may be defined as vulnerable. We investigate the vulnerability of a model of the fisheries system in Lake Superior to invasion by sea lamprey (*Petromyzon marinus*).

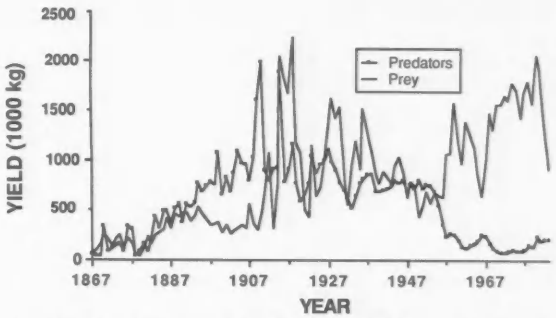

FIG. 1. Yield series of the Ontario commercial fishery of prey and predatory species. The prey group includes lake herring, chubs, rainbow smelt, lake whitefish, round whitefish, and suckers. The predator group includes lake trout, walleye, and northern pike. Data from Baldwin et al. (1979).

The Model

To model the system, we divided the major commercial fish species from Lake Superior (Baldwin et al. 1979) into two groups: predators and prey. The group of predators included lake trout (*Salvelinus namaycush*), walleye (*Stizostedion vitreum*), and northern pike (*Esox lucius*), and it was dominated (as measured by the amount of commercial yield) by lake trout. The prey group included lake herring (*Coregonus artedii*), chubs (which may have included *C. nigripinnis*, *C. zenithicus*, *C. reighardi*, and *C. hoyi*), rainbow smelt (*Osmerus mordax*), yellow perch (*Perca flavescens*), lake whitefish (*C. clupeaformis*), round whitefish (*Prosopium cylindraceum*), and suckers (*Catostomus* and *Moxastoma spp.*) and was dominated by lake herring. We then used the predator–prey model introduced by May et al. (1979) to describe the dynamics in the fishery:

$$(1)\quad dN_1/dt = N_1(C_1 - a_{11}N_{11} - a_{12}N_2)$$

$$(2)\quad dN_2/dt = N_2(C_2 - a_{21}N_2/N_1)$$

where N_1 denotes the prey population density, N_2 denotes the predator population density, and C_1 and C_2 are constants which include system structure and harvesting (e.g. recruitment rate, as affected by population densities and fishing effort). We used constant effort simply because prior to invasion by lamprey there was little regulation of the fishery, and we assumed that maximum effort was applied by the fishers.

To investigate the suitability of modeling the system as a predator–prey, we plotted the time series of commercial yield for both the prey and predator groups (Fig. 1). We then calculated the partial correlations between and within the time series with lags of up to 24 yr (Box and Jenkins 1976; SAS Institute Inc. 1982). The only significant ($p \leq 0.05$) partial correlation (=0.51) between the predator and the prey time series was with the predator leading the prey by 5 yr. In other words, high yield from the predator group resulted in high yield from the prey

group 5 yr later. Note that 5 yr corresponds to the average age of recruitment of many fish species in Lake Superior (Scott and Crossman 1973). This result is expected if there is a predator–prey interaction in the community and if high yield from predators reduces the density of predators. Thus, we concluded that the predator–prey model (1) and (2) is a reasonable approximation of the dynamics of the Canadian fishery in Lake Superior.

After invasion by lamprey, (1) and (2) were modified to

$$(3)\quad dN_1/dt = N_1(C_1 - a_{11}N_1 - a_{12}N_2 - u_1) \quad 0 \leq u_1 \leq u_{1\max}$$

$$(4)\quad dN_2/dt = N_2(C_2 - a_{21}N_2/N_1 - u_2) \quad 0 \leq u_2 \leq u_{2\max}$$

where u_1 represents the increase in effort on the prey species due to decrease in abundance of predatory species (i.e. a fisheries shift) and u_2 reflects the increase in death of predatory species by the invasion of sea lamprey. Since there are physical limitations on the magnitude of both effort and death due to lamprey predation, both u's are bounded.

Next, by setting

$$x_1 = N_1(a_{12}/a_{21}),\ x_2 = N_2(a_{12}/C_1),\ \tau = tC_1$$

$$\beta = a_{11}a_{21}/(C_1a_{12}),\ \gamma = C_2/C_1$$

$$S_1 = u_1/C_1$$

$$S_2 = u_2/C_1,$$

the system (3) and (4) became dimensionless, and we obtained

$$(5)\quad \dot{x}_1 = x_1(1 - \beta x_1 - x_2 - S_1) \quad 0 \leq S_1 \leq S_{1\max}$$

$$(6)\quad \dot{x}_2 = x_2(\gamma - x_2/x_1 - S_2) \quad 0 \leq S_2 \leq S_{2\max}$$

where superior dots denote derivatives with respect to τ.

Results

The parameters remaining in (5) and (6) are related to environmental effects mainly through C_1 and C_2. Local stability analysis indicated that decreasing β or decreasing γ will decrease stability. The vulnerability of x_1 and x_2 to extinction, according to the model, is related to these parameters and thus indirectly to environmental changes. We will not explore this point further. For this analysis, we will assume that β and γ are fixed and simply compare the change in vulnerability of the system due to the invasion by lamprey. The overall averages of yield (in thousands of kilograms) of predatory and prey species before the invasion by sea lamprey were 650 and 680, respectively (see Fig. 1). Therefore, we concluded that γ is on the order of 1. Note that β represents density-dependent effects within the populations (i.e. when the prey is not regulated by density, then $a_{11} = 0$, which yields $\beta = 0$).

To investigate the vulnerability set of the simplified fish community (where all predatory and all prey species were lumped together), we assumed the following scenario. The maximum possible increase in the mortality of prey species due to increase in fishing effort (because of the decrease in abundance of the predatory species whose mortality was increased by lamprey invasion) was set to $S_{1\max} = 0.2$. Similarly we fixed the maximum increase in mortality of predatory species due to lamprey invasion to $S_{2\max} = 0.2$. Furthermore, we set $\beta = \gamma = 0.5$ (the vulnerability analysis was insensitive to changes in these parameters within an order of magnitude). The vulnerability set for this scenario is shown in Fig. 2. Next, we assumed that the lamprey's predation on the predatory species in our system increased to a possible maximum $S_{2\max} = 0.4$ (Fig. 3). Note that the range of possible densities of the prey species (x_1) has

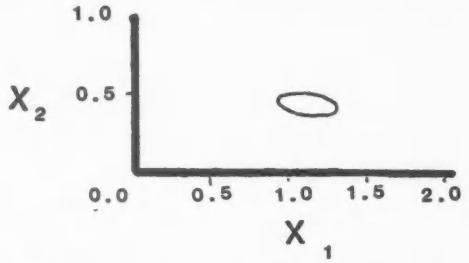

FIG. 2. Vulnerability set for the following parameters according to eq. (5) and (6): $\beta = 0.5$, $\gamma = 0.5$, $S_{1\max} = 0.2$, $S_{2\max} = 0.2$ where x_1 refers to prey species and x_2 to predatory species.

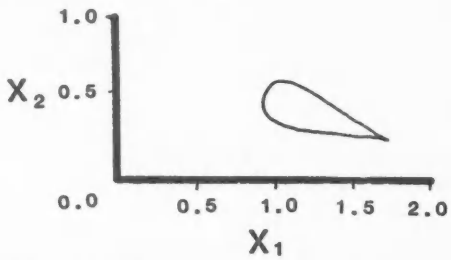

FIG. 3. Vulnerability set for the following parameters according to eq. (5) and (6): $\beta = 0.5$, $\gamma = 0.5$, $S_{1\max} = 0.2$, $S_{1\max} = 0.4$ where x_1 refers to prey species and x_2 to predatory species.

increased with increased predation pressure by lamprey (on the predatory fish species). Yet, the minimum possible density remained around 1.0. For the predatory species the range of possible densities increased as well, but with the minimum possible density decreasing from about 0.4 to around 0.25 (Fig. 2 and 3). This result means that with the invasion of sea lamprey and decrease in the abundance of predatory fish species (primarily lake trout) the predatory species became more vulnerable to extinction, but the vulnerability of prey species to extinction remained unchanged. This conclusion is intuitively clear, but with the aid of this analysis some quantitative conclusions are reached.

Discussion

Our analysis relies on a mathematical model which must approximate dynamics in the real system. The fact that (a) the yield time series exhibit partial correlation with the prey species lagging the predatory species by 5 yr, (b) the average age at recruitment for many species is about 5 yr, and (c) the model dynamic is insensitive to changes (by an order of magnitude) in parameter values lends credibility to the predator model (5) and (6) and to our analysis. Furthermore, (a)–(c) refute the claim by many Great Lakes fishery biologists and managers that the yield data are too noisy and thus of limited usefulness.

We derived the minimum possible density that the prey species can reach when the predation pressure by lamprey on the predatory species increased from $S_{2\max} = 0.2$ to $S_{2\max} = 0.4$ (eq. (6)). Note that the system (5) and (6) is globally stable (Goh 1980) in the sense that both densities of prey and predatory species will remain in the positive orthant for all times. If we were to increase $S_{2\max}$ further, the approach of the boundary of the vulnerability set to the x_1 axis would have been asymptotic. In other words, the minimum possible density for the predatory

species will never be zero. However, a stock smaller than some minimum size can be considered effectively extinct..

More realistic models should include an increase in the maximum possible perturbation on the prey populations death rate ($S_{1\,max}$), as a result of increasing death of the predatory populations due to invasion by sea lamprey ($S_{2\,max}$). In other words, as the abundance of predatory species was reduced by lamprey, the fisheries started to shift to the prey species. Thus, the addition of fisheries dynamics to the system renders the predator populations even more vulnerable to extinction than indicated by our analysis because the shift in fisheries effort effectively reduced the abundance of food for predators. Overall, the predatory fish species in Lake Superior were affected by two synergistic disturbances: lamprey predation and a decreased food base due to the shifting fishery.

We view vulnerability analysis as a useful tool for analysis of management options and the effect of perturbations with known bounds but unknown temporal distribution on population densities. There are several advantages to using vulnerability analysis in the present context over the more traditional stochastic dynamic models: (1) No assumption is made about the distribution of the disturbance. Thus, the analysis in effect admits modeling as well as random errors. Stochastic models rarely admit modeling errors, and therefore must be verified by residual analysis. (2) The approach is deterministic, and therefore, analytical solutions are more readily available. Stochastic modeling becomes intractable very quickly, with analytical solutions available in few cases only. Thus, qualitative analysis is easier with vulnerability analysis. (3) Many fisheries models are discrete, and vulnerability analysis for discrete-time systems is now possible (Grantham and Fisher 1987). (4) The analysis leads naturally to management under uncertainty (see Vincent 1987).

Spectrum Analysis

Introduction

In this section we briefly present an intuitive outline and common terminology of spectrum analysis. Spectrum analysis is based on the fact that every function $f(t)$, where t may be continuous or discrete, can be decomposed into a series of sine waves (the so called Fourier series) whose sum will approximate $f(t)$ in a least-squares sense. If $f^*(t)$ is a least-squares approximation of $f(t)$, then $f^*(t)$ can be expressed as

$$(7)\quad f^*(t) = a_0/2 + \sum_{k=1}^{K} a_k \cos(k\omega_0 t + \alpha_k)$$

where ω_0 is the so-called fundamental frequency (Bloomfield 1976) determined so that the period of $f(t)$ is $2\pi/\omega_0$, k is the so-called harmonic number (e.g. $k = 1$ is termed the first harmonic, etc.), and a's and α's are least-squares coefficients (arbitrary real numbers which are the parameters chosen such that the mean sum of squares of the residuals of $f^*(t)$-$f(t)$ is minimized). Thus, ignoring phase lags, which are expressed in the α's, the function in the time domain, $f(t)$, can be characterized in the frequency domain by amplitude as a function of the harmonic number. For example, time series data such as in the upper curve of Fig. 4A can be decomposed into two sine waves (lower curves, Fig. 4A), each characterized by its unique frequency and amplitude. In the frequency domain (Fig. 4B), each of the component waves is plotted in amplitude versus harmonic number k from eq. (7). Real time series are not as well behaved as illustrated in Fig. 4A. Thus, K, the number of coefficients to be fitted in order to meet the least-squares criterion, will usually be larger than 2. In other words, more "jagged" data series require larger values of K in order to meet the least-squares criterion. For larger K, more parameters (a_k and α_k) need to be calculated (eq. (7)).

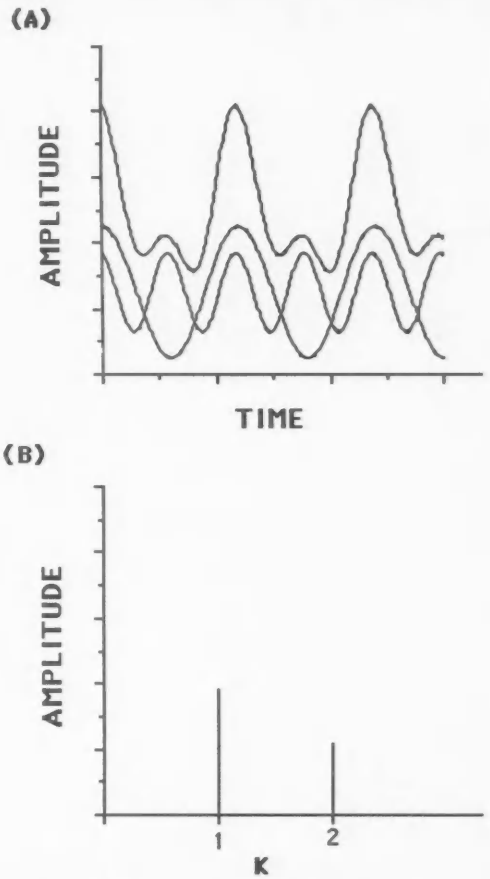

FIG. 4. Basic ideas of spectrum analysis. (A) Upper curve represents a hypothetical time series; lower two curves represent the decomposition of the upper curve; the sum of the two, at each point along the time axis, gives the upper curve. (B) Lower two curves in Fig. 4A are represented in frequency domain, the so-called power spectrum in terms of amplitude (a_k) versus the harmonic number, k. Ordinate units are arbitrary.

Univariate spectrum analysis should reveal single species characteristics. These characteristics are essentially described by two variables: amplitude and frequency. For example, a species may exhibit large amplitudes at low frequencies (its fluctuations will be slow, with large changes in abundance) or small amplitudes at low frequencies. May (1984) argued that the abundance of species at higher trophic levels should fluctuate more slowly (at lower frequencies) than those lower on the trophic level. The amplitude of fluctuations (the magnitude of fluctuations in density) of species at higher trophic levels should be smaller than that of species of lower trophic levels. Changes in the amplitude and frequency of fluctuations (in say abundance of species, or in yield), following a perturbation, should reflect qualitative changes in the fisheries.

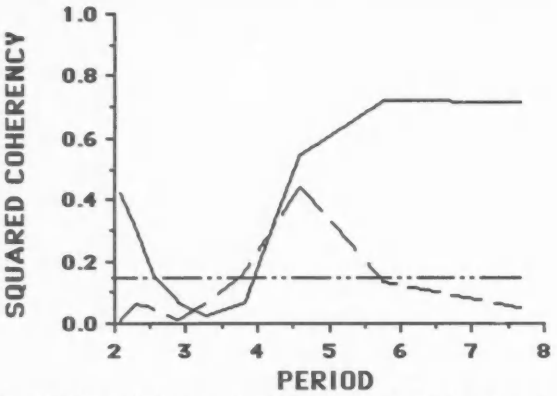

FIG. 5. Coherencies between the yield time series for lake herring and lake trout before (solid line) and after (broken line) invasion by sea lamprey to Lake Superior. Coherencies below the horizontal line are insignificant ($p \leq 0.05$). Period is in years.

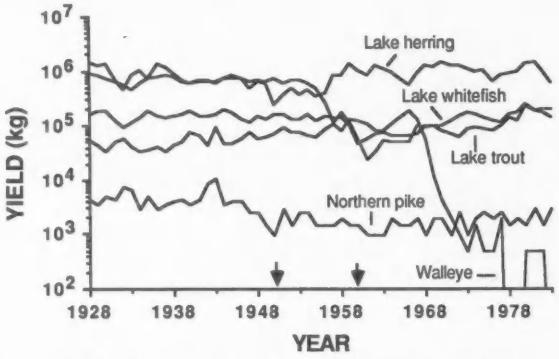

FIG. 6. Yield series of the Ontario commercial fisheries of various species. Left of the first arrow is considered the pre-lamprey period and right of the second arrow is the post-lamprey period. Data from Baldwin et al. (1979).

When two series are Fourier transformed, as in multivariate spectrum analysis, they can be correlated over the various frequencies to give a quantity termed coherency, which is between 0 and 1. Much like the coefficient of determination of regression (R^2), the squared coherency indicates how closely two series are fluctuating at a particular frequency. It is a measure of the synchrony of fluctuations between two time series. In other words, a coherency is derived for each of the frequencies embedded in both time series. At each of these frequencies the correlation between amplitudes of fluctuations gives the coherency at that particular frequency. For example, the change in coherencies between the yield series for lake herring and lake trout over various frequencies before and after invasion by sea lamprey is illustrated in Fig. 5. Obviously, before the invasion by lamprey, at periods of over 4 yr per cycle (where cycle is defined as the length of time between two peaks in yields), the series of both species were well synchronized (the amplitudes are significantly correlated). At periods of around 3 yr per cycle the coherencies were insignificant (the fluctuations in yield of the two species were not synchronized).

When considering a community of more than two species, the coherencies between pairs of species, much like correlation coefficients (Evans and Waring 1987), do not lend themselves to simple interpretation because of the masking effect of coherencies of each member of the pair with other species in the community. To remove this effect, paired partial coherencies over the various frequencies $\rho_{ij}(\omega)$, $i, j = 1, \ldots, 5$ were calculated (Hannan 1970, p. 261). These can be interpreted as the coherency between a pair of species which remains after removing that part of the coherency between the pair which is accounted for by coherencies between each member of the pair and the rest of the species in the community. $\rho_{ij}(\omega)$ then reflects the true synchronization between the fluctuations in yield from species i and species j at various frequencies. If major perturbations to a fish community result in changes in the synchronization of commercial yield of species over time, these changes should be detected by multivariate spectrum analysis.

Methods

Univariate and multivariate spectrum analyses (Hannan 1970; Priestly 1981) were applied to the Ontario commercial fisheries data from Lake Superior (Baldwin et al. 1979 and Fig. 6). We divided the data into periods of before and after the invasion by sea lamprey (Fig. 6). This invasion is considered a major perturbation to the fisheries system in Lake Superior (Lawrie and Rahrer 1973). Since the fisheries system was going through some adjustment period just after the invasion, we arbitrarily divided the data into yield series before (1928–50) and after (1961–83) the invasion, excluding a period of 10 yr during which the community was adjusting, presumably, to the new perturbation and when lamprey control had limited effect.

To observe the characteristic frequencies and amplitudes, we calculated the periodograms for each species with SAS (SAS Institute Inc. 1982). Since these periodograms showed a significantly high amplitude at one particular frequency for each species, we chose this frequency (with its associated amplitude) as characterizing the yield series for a species. If a point in the frequency domain plane, which is determined by the frequency–amplitude pair, after invasion by lamprey differed from the point before invasion for a particular species, we concluded that the yield series of that species changed (qualitatively) due to the perturbation and all of its associated effects (e.g. shifting in fisheries effort due to changes in catch, etc.).

Since the behavior of the yield series in the frequency domain for a single species (i.e. the spectrum) is generally different from the combined behavior for pairs of species (i.e., the cospectrum), we calculated partial coherencies, $\rho_{ij}(\omega)$, for the five major commercial fish species in Lake Superior (Baldwin et al. 1979 and Fig. 6). To typify community-wide changes, we chose, for each pair of species, that frequency for which ρ was highest and significant ($p \leq 0.05$) before or after invasion by sea lamprey. The periods of these frequencies were rounded to the nearest year. Significant changes in ρ's from before to after invasion (+ or −, Table 1) indicated that the coupling of fluctuations in yield changed. Presumably, if the change in ρ was not significant, then the coupling between the yield series of two species did not change. To identify the relationships between the synchronization in fluctuations between a particular species and the rest of the community, we summed the significant ρ's for each species (Table 2). Thus, for example, the amount of synchronization between lake herring and the rest of the community was calculated as $0.88 + 0.73 + 0.70 = 2.31$. This measure then summarizes the extent to which the yield series for a particular species is coupled with the yield series for all other species in the community.

TABLE 1. Partial coherencies for the yield series between pairs of species before and after the invasion of Lake Superior by sea lamprey (data are for Ontario waters only). The periods (1/frequencies) with significant partial coherencies before and after the invasion were chosen as characterizing the temporal aspects of interspecific interactions (see text for further explanation). Asterisks indicate significant partial coherencies ($p \leq 0.05$) (Hannan 1970, p. 261). All changes in partial coherency were significant ($p \leq 0.05$), as tested according to Hannan (1970, p. 262).

Pair	Period (yr)	Partial coherency before	Partial coherency after	Change
Lake herring and:				
lake whitefish	2.0	0.88*	0.24	−
lake trout	2.0	0.73*	0.13	−
northern pike	2.0	0.20	0.46*	+
walleye	7.0	0.70*	0.33	−
Lake whitefish and:				
lake trout	2.0	0.12	0.88*	+
northern pike	2.0	0.29	0.50*	+
Lake trout and:				
walleye	2.0	0.24	0.52*	+

TABLE 2. Sum of significant partial coherencies between a species and the rest of the community (Table 1) for before and after invasion by lamprey. Asterisks define "keystone" species.

Species	Before	After
Lake herring	2.31*	0.46
Lake whitefish	0.88	1.38*
Lake trout	0.73	1.40*
Walleye	0.70	0.52
Northern pike	0.00	0.96

Results

The frequency–amplitude coordinates for five species of the Ontario fisheries from Lake Superior were plotted (Fig. 7). Each species is represented by two points (before and after invasion by sea lamprey) and an arrow which indicates the direction of change from before to after the invasion. For each species, amplitudes were standardized by the total sum of amplitudes in the power spectrum of that species. The following results pertain to comparisons of the time series with before and after the invasion: (1) both frequency and amplitude of fluctuations of the yield series for lake trout decreased; (2) amplitude of fluctuations of the yield series of walleye increased, without changes in frequency; (3) yield of lake herring did not change much; and (4) yield of northern pike changed primarily due to increase in frequency. Thus, except for lake trout, the yield series of all species increased in either frequency or amplitude, or both.

Overall, the synchronization of fluctuations in yield series (as measured by the value of the partial coherency) did not change much after the invsion by lamprey; i.e. the column sums in Table 2 were 4.62 and 4.72 for before and after the invasion. Yet, upon examination of the details of pairs of interactions, a clear pattern emerged. For lake herring, whose partial coherencies with the rest of the community were highest (2.31) before invasion by lamprey (Table 2), all of the partial coherencies became smaller (Table 1) (except with northern

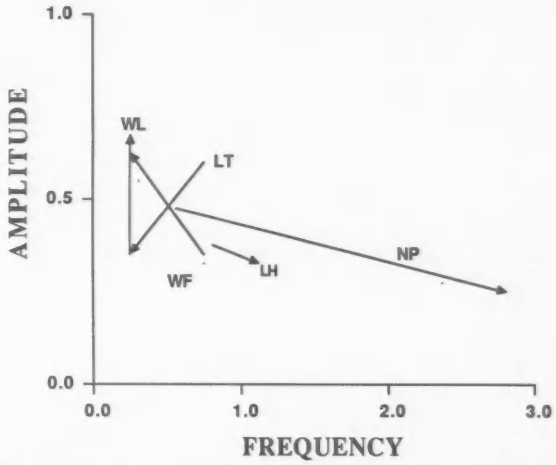

FIG. 7. Changes in amplitude and frequency characteristics of the yield series for five fish species from the Ontario fisheries from Lake Superior after the invasion by sea lamprey. For each yield series, the highest amplitude at a particular frequency was chosen as characterizing the yield series. The arrows begin at the frequency–amplitude pair before the invasion and end at the pair after the invasion. LH = lake herring, LT = lake trout, WL = walleye, WF = lake whitefish, NP = northern pike. Each species' amplitudes were standardized by the sum of amplitudes of that species' power spectrum. Frequency is in radians per year.

pike, which, in terms of yield, is a minor component of the community). In other words, the synchrony between the yield series of lake herring and the rest of the community became disrupted. Furthermore, after the invasion by lamprey, lake whitefish and lake trout became dominant in terms of their ρ's with their partial coherencies more evenly distributed among the species (Table 1) compared with before lamprey invasion.

Discussion

To investigate community-level reaction to invasion by lamprey, we calculated the partial coherencies between pairs of yield series. Species with the highest sum of ρ's with the community may be regarded as "keystone" species, in a sense that their yield time series is synchronized with the rest of the yield time series more than any other species in the fishery. One might postulate that disruption in the yield of keystone species could cause the collapse of the fishery more than the disruption in yield of other species in the fishery. This point merits further investigation.

From a management standpoint, our analysis indicates that even though the invasion by sea lamprey resulted in a decline in the yield of lake trout more than any other species, much of the cyclicity of the community, and therefore predictability of yield, was related to the cyclicity of yield from lake herring before the invasion by lamprey. After the invasion, synchrony became more diffuse and was related mostly to the yield from lake whitefish and lake trout. Since, as discussed as ASPY, one of the management goals for the fish community in Lake Superior is the return, as much as possible, to pre-lamprey community characteristics, our recommendation is to pay special attention to management (through regulation and other means) of lake herring.

No major change in the yield from lake herring has occurred in Ontario waters before and after the invasion. Yet, extinction

of local stocks could have happened (e.g. as demonstrated for the Wisconsin waters by Selgeby 1982), and proportionately more "prey" species (primarily lake herring) than predatory species have been harvested since the 1950's (Fig. 1). Thus, if interspecific interactions are spatially dependent, local extinctions of lake herring may result in a community-wide disruption in synchrony of commercial yield. Therefore, spatial stabilization of the yield from lake herring should be sought. This point merits further investigation. Perhaps one way to speed up the rehabilitation of lake trout populations is to insure that the future spatial distribution of lake herring is as close as possible to what it was before the invasion by sea lamprey. This may be accomplished by an overall reduction in the harvest of lake herring and by imposing specific quotas (or better yet, specific efforts) to specific lake herring fishing grounds.

One needs to keep in mind that the emerging pattern from this analysis cannot be interpreted in biological terms only. The data for yield series reflect many other factors which occurred in Lake Superior since the early 1900's. Furthermore, they reflect fishers' behavior. For example, since whitefish and lake trout are caught in the same gear in similar places, we expected that both of these will behave similarly. Surprisingly, their ρ's were insignificant before and became highest (compared with the ρ's of other species) after the invasion by sea lamprey. Thus, the analysis herein pertains to the fisheries system as a whole, and not to its biological aspects only.

We should emphasize that in looking for patterns within large systems, and in calculating many parameters (such as R^2 or ρ), one may expect some to be significant by chance alone. We do believe, however, that our results (Table 1) are not spurious for two reasons: (1) we calculated the ρ's, thereby removing potential inputs from coherencies with other species; and (2) one can hardly expect spurious ρ's to be as high as some of those we found (e.g. 0.88, 0.73). Similar investigation for the other Great Lakes would reveal how general these patterns are.

Finally, a word of caution. The time series upon which our analysis relies is short for spectrum analysis, and at present it is difficult to obtain an estimate of how sensitive our results are to the length of the time series. Rather than conclude that because of their length the data should not be analyzed, we view our analysis and results as preliminary. We hope to extend our analysis to include longer time series, and data from the other Great Lakes.

Acknowledgments

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Predicting Great Lakes Fish Yields: Tools and Constraints[1,2]

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Prediction of yield is a critical component of fisheries management. The development of sound yield prediction methodology and the application of the results of yield prediction are central to the evolution of strategies to achieve stated goals for Great Lakes fisheries and to the measurement of progress toward those goals. Despite general availability of species yield models, yield prediction for many Great Lakes fisheries has been poor due to the instability of the fish communities and the inadequacy of available data. A host of biological, institutional, and societal factors constrain both the development of sound predictions and their application to management. Improved predictive capability requires increased stability of Great Lakes fisheries through rehabilitation of well-integrated communities, improvement of data collection, data standardization and information-sharing mechanisms, and further development of the methodology for yield prediction. Most important is the creation of a better-informed public that will in turn establish the political will to do what is required.

La prédiction du rendement est une composante critique de la gestion des pêches. La mise au point d'une méthode fiable de prédiction du rendement et l'application des résultats servent de pierre angulaire à l'élaboration de stratégies pour réaliser les buts visés de la pêche dans les Grands Lacs et à la quantification du progrès réalisé dans ce sens. Malgré que des modèles du rendement spécifique soient généralement disponibles, la prédiction du rendement de nombreuses pêches dans les Grands Lacs a eu peu de succès à cause de l'instabilité des communautés piscicoles et de l'insuffisance des données recueillies. Une multitude de facteurs d'ordre biologique, institutionnel et social restreignent la mise au point de prédictions fiables et leur application à la gestion. Un pouvoir de prédiction amélioré requiert une stabilité accrue des ressources dans les Grands Lacs par le rétablissement de communautés bien intégrées, l'amélioration de la collecte de données, le normalisation des données, les mécanismes de diffusion de l'information et le perfectionnement des méthodes de prédiction du rendement. Au premier rang vient la sensibilisation du grand public qui amènera les autorités politiques à agir dans ce sens.

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Understanding yield processes sufficiently to enable the prediction of future yields with acceptable accuracy has long been the aim of fisheries managers. Accurate prediction of yield in the Great Lakes is important for at least two reasons: (1) to facilitate management of the fisheries and (2) to enable fisheries managers to track the trajectory of Great Lakes fisheries in their progress toward rehabilitation.

Many papers contributed to this symposium have in some way dealt with yield prediction. We here review the extant methods of yield prediction, evaluate their relative merits in the context of Great Lakes fisheries, and discuss the constraints on the development and use of meaningful near-term forecasts.

Need for Reliable Predictions

Decision-makers in the Great Lakes region require reliable yield prediction methodology as a key component of the fisheries management process. Prediction of fish yield plays a

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central role as individuals from various jurisdictions work together to establish common goals for the development of fish communities in each lake, develop appropriate strategies to meet those goals, and produce information to measure progress and evaluate strategies. The need is especially critical within the context of current fisheries rehabilitation efforts.

Reliable yield prediction methods are furthermore important for managers trying to transcend reactive decision-making: confidence in the method allows a more forward-looking approach to management, and at the same time assists in the development of interagency consensus. Success in applying the method develops essential public confidence and support.

Although the need for sound methodology is clear and undisputed, the application of existing methodologies has been less than totally successful.

Predictive Approaches

Approaches to yield estimation can be generally classified into two distinct categories: (1) mathematical–biological models that produce theoretical results and (2) empirical relations between potential yield and certain characteristics of the ecosystem (Deriso 1987). The latter approaches, which generally address long-term yield prediction, were reviewed by Leach et al. (1987) and will not be considered further here. The former category includes surplus yield (production) models, analytical (dynamic pool, age-structured) models, and hybrid models, all of which are used to predict near-term yields. These models are based on the assessment of a stock's capacity to withstand withdrawals of biomass (Shuter and Koonce 1988) and are commonly used to generate catch quotas. Four elements are required for the use of these models: (i) raw data from the stock, (ii) estimates of stock characteristics, (iii) a quantitative description of the productive capacity of the stock, and (iv) a set of objectives that a quota management system must achieve (Shuter and Koonce 1988).

Surplus yield approaches have undergone considerable development since Schaefer's (1954) classical model. Walter (1973) developed a practical modification by adding time delays. This refinement overcomes the need for the population to be in equilibrium. However, a long time series of data for consecutive years is required. The major disadvantage of the Walter time delay model is that it works best as a post hoc analysis and is less reliable for predicting stock changes associated with current large changes in fishing rates (Pitcher and Hart 1982). Beddington and May (1977) further refined the surplus yield model to include random environmental effects and demonstrated that the variability of yield increases as maximum sustainable yield is approached (Pitcher and Hart 1982). Further development by Schnute (1977) has dealt with fitting the surplus yield model in the presence of environmental randomness and deriving confidence limits for the yield and fishing effort values.

Surplus yield models have modest data requirements (catch and effort time series) and are relatively simple to use. However, they provide only a limited description of stock behaviour because they do not include information on the effects of age or size structure. In addition, the assumptions inherent in these models (that catch-per-unit-effort and effort data are reliable indicators of the abundance of the exploited portion of the stock and the exploitation rate, respectively) are often violated. An additional disadvantage of surplus yield models is that effective functioning of the fitting procedures requires a large degree of contrast in the data (stock size) (Shuter and Koonce 1988). Such contrast is usually difficult to obtain.

Analytical (dynamic pool) models (Beverton and Holt 1957) incorporate two improvements that lead to a more realistic approach. First, the processes that influence fish biomass are explicitly described as model components. Second, the age structure of the stock is included. Thus the processes of growth, recruitment, natural mortality, and fishing mortality can be modelled to operate independently on each age group. Modern analytical models incorporate a general yield equation, resulting in increased flexibility of the model to suit a variety of fisheries and to predict yields from fisheries with changing exploitation rates (Pitcher and Hart 1982).

Analytical models provide a more comprehensive description of stock behaviour, but they require extensive and costly data. Assumptions inherent in these models can be evaluated, but use of the models can be relatively complex. Again, there is difficulty in obtaining data over a wide range of stock sizes, a condition necessary for fitting stock–recruitment relations (Shuter and Koonce 1988).

Koonce and Shuter (1987) suggested that, if data are available, detailed population models are preferable to surplus yield models. Surplus yield models appear to pose a greater risk of providing misleading information that results in fishery collapse, and there are persistent problems with parameter estimation. There has been some recent work on "hybrid" models (Deriso 1980; Csirke and Caddy 1983), which overcome some of the weaknesses of surplus yield models, yet are not as demanding of data as are analytical models. However, such hybrids have not often been applied (Shuter and Koonce 1988) and their performance has not been evaluated.

Analytical and surplus yield models, such as those presented at this symposium by Deriso (1987), Jacobson et al. (1987), B. E. Skud (unpubl. data), and others, have been single-species approaches. However, there is increasing awareness of the role of community interactions in determining species yields (Mercer 1982; Mahon 1985). Interest in forage base (Kitchell and Hewett 1987) and ecosystem modelling (T. Laevastu and N. Bax, unpubl. data) indicates a more holistic approach to yield assessment that is long overdue. Recent attempts have been made to adapt existing mathematical models to a multispecies framework (Deriso 1987; Pikitch 1987; Daan 1987), but these are as yet inadequate to provide required information for fisheries management (Daan 1987). Koonce and Shuter (1987) suggested that until process and observation error associated with stock assessment can be reduced, information on community interactions is unlikely to improve the ability of decision-makers to manage effectively (see also G. R. Spangler and J. J. Collins, unpubl. data). In addition, improved understanding of environmental effects on single stocks will be required before multispecies approaches will provide useful models (e.g. see Taylor et al. 1987).

Current Use of Yield Prediction Models for the Great Lakes

Short-term forecasting (1- to 3-year time frame) is the most critical need for fisheries managers in the Great Lakes region. Rational, defensible procedures for determining total allowable catch (TAC) are required for a number of species. Methods currently being used for determining TACs vary among lakes, species, and agencies.

For Lake Erie walleye (*Stizostedion vitreum vitreum*), data on

abundance of young-of-the-year and annual withdrawals, collected by provincial, state, and federal agencies, are used to update annually a sequentially projected standing stock model. The model provides recommended quotas for the following year ($t + 1$), and provisional quotas for year $t + 2$, based on allowable fishing mortality rate established by an interagency committee of the Great Lakes Fishery Commission (Hatch et al. 1987). For Lake Erie yellow perch (*Perca flavescens*), an age-structured model has been developed to determine an optimum fishing mortality, which is used, along with annual estimates of stock size, to determine TACs (Baker et al. 1985; M. Petzold, Algoma Fisheries Assessment Unit, Sault Ste. Marie, Ont., pers. comm.). For yellow perch in the Ontario waters of Lake Ontario, a surplus yield model is applied (W. Dentry, Lake Ontario Fisheries Unit, Picton, Ont., pers. comm.). Quotas for lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), and ciscoes (chubs) (*Coregonus* spp.) for certain United States waters are generally determined using age-structured models (R. W. Hatch, unpubl. data). Yield estimation for other species or waters is severely limited by shortcomings in available data. Time series of catch and effort data are generally short or limited to commercial operations, and data on population parameters are sparse. For many Ontario stocks in Lake Superior and Lake Huron, recent quotas have been allocated on the basis of historical catches (the "best 3 yr out of the last 5"), and quota amendments are based on estimates of year-class strength (R. Payne, L. Huron Fisheries Assessment Unit, Owen Sound, Ont., pers. comm.) or indicators of abundance, fecundity, growth, and age structure of the fishable stock (W. MacCallum, Lake Superior Fisheries Assessment Unit, Thunder Bay, Ont., pers. comm.).

Constraints on Prediction of Yield

Despite the general availability of single-species models to predict fish yields, it is apparent from the papers presented during this symposium that these models are not satisfactory for many Great Lakes situations. In general, yield prediction to date has been largely inadequate due to a multidimensional set of constraints on the development of accurate, meaningful forecasts. These constraints have their origins in the biological, institutional, and societal elements that comprise the Great Lakes fisheries.

Much of the difficulty encountered in attempting to apply available models stems from the lack of adequate knowledge. This lack derives in part from a high degree of biological uncertainty inherent in current Great Lakes fisheries. The present fish communities are considered "astatic" (Ryder and Kerr 1978, and unpubl. data), producing highly variable and therefore highly unpredictable yields, relative to historic trends.

Additional difficulty relates to a community structure and interspecific dynamics that are vastly different from their historical counterparts. Fish yields from changed fish communities and altered habitats may bear no similarity to historical yields from communities of indigenous species. Since many models are based on the assumption that one may predict the future by observing the past, the lack of historical yield data from these new assemblages may be critical.

The extensive data requirements of many yield models are difficult and costly to satisfy. Fisheries management commitments preclude the kind of manipulations necessary to examine stock behaviour over a wide range of stock sizes. Generally, even the best yield prediction methods are currently limited by a lack of good estimates of prerecruit abundance and survival, and a lack of reliable catch data, especially for species exploited jointly by commercial and recreational interests. Quantification of angling yield from large bodies of water is difficult and expensive. Illegal harvest of premium-priced species is known to be substantial, but its quantification is obviously impossible. In addition, estimates of changes in catchability over time are scarce. Critical assessment programs are lacking due to the inadequacy of funds, and mechanisms for standardizing and integrating information from various agencies into a common data base are insufficient, due to the complex intergovernmental framework in the Great Lakes Basin (Francis et al. 1979). The lag time between the perturbation of a system and its visible manifestation in the fishery (Loftus and Regier 1972) imposes an additional constraint that affects assessment capability and hence the ability to predict short-term yields (although Cohen et al. (1987) provide an example from Lake Superior in which time-series analysis generates useful predictions of catch from very limited catch and effort data).

Current approaches to stock management may also constrain acquisition of new knowledge. Rehabilitation of lake trout has been essentially unsuccessful, apart from Lake Superior, despite the Great Lakes Fishery Commission goal of rehabilitation (Anonymous 1983). It is suspected that the poor results relate to inadequate control of the fishing mortality imposed on lake trout stocks (W. L. Hartman, unpubl. data), although community resistance (Pimm and Hyman 1987) may also play a role. Some formerly abundant stocks may now be locked into a lower "domain of stability" (Colby 1984). However, continuing high fishing mortality on lake trout renders the full assessment of such a theory impossible. Certainly the current high levels of fishing mortality may mask other important factors such as habitat limitations and predation (Eshenroder et al. 1984). Reduction of fishing mortality on lake trout is essential to an evaluation of the potential for community restructuring.

Knowledge is also lacking on the persistence and resilience aspects of the stability problem. Except for the simplest cases, there is no understanding of how systems persist under harvesting or other perturbations (Pimm and Hyman 1987), although there is general agreement that rehabilitated Great Lakes fish communities would require few external inputs to remain highly persistent.

Ultimately, even the best available yield models may be inadequate. Lack of tested multispecies or community approaches constrains managers' ability to make yield predictions for systems where forage abundance affects several exploited species. Development of new yield prediction theory, a major thrust of this symposium, is urgently needed.

Constraints on Application of Yield Predictions

Lack of new methodology, and of data that enable the use of existing methodology, is only part of the yield prediction problem. Numerous constraints on the use of yield forecasts limit the effectiveness of existing science. Slow institutional response time (Peyton 1987) and institutional inertia, conflicting management policies, and the complex governmental framework in the Great Lakes Basin (Francis et al. 1979; B. E. Skud et al., unpubl. data) all contribute to difficulties in application of yield information.

Slow response time appears to be endemic to bureaucracies. Lags are evident at every step of the problem-solving process, from recognition and detection through data-gathering and the

analysis needed for administrative action. The result is often that fishery management programs follow trends rather than generate new trends (McFadden 1969).

The Ontario Ministry of Natural Resources (1976) characterized this sequence as "reactive decision-making" that deals with problems and not with opportunities. Lagging responses are particularly critical when one is dealing with salmonid problems over innately long periods of time.

Institutional inertia is another serious constraint that may take several forms. It is easier to maintain programs already in place and add to them than to reallocate resources for new programs that might yield better results (Ontario Ministry of Natural Resources 1976). Agencies are frequently locked into programs that influence future decisions and allocation of funds. This form of inertia is usually internally imposed. There is also an externally imposed inertia that leads to frequent directional changes in programs and policies. Relatively frequent changes of elected and appointed leaders are almost invariably accompanied by a "mandate" for new initiatives, often leaving existing, underfunded programs no better off (Loftus 1987). Change in direction often collides with endemic resistance to change by agencies, further extending institutional response time.

Conflicting management policies among the many agencies with vested interests in Great Lakes resources are also a problem. Two to five provincial or state governments have primary management responsibilities on each of the Great Lakes (Francis et al. 1979). The Great Lakes are shared internationally, and thus involve two federal governments. Policies of these agencies are integrally tied to the economic and social fabric of the public that these agencies serve, and thus may be in conflict. The framework for dealing with conflicting agency policies is tenuous. The Great Lakes Fishery Commission was formed for this purpose (Fetterolf 1980) and has achieved some remarkable success. However, the Commission's goal of balanced fish communities supported by natural reproduction has not yet been attained (Fetterolf 1980). There is still a risk that without broad consensus on the composition of desirable fish communities, independent management agencies will choose their own direction when short-term political or economic goals are in conflict. The 1980 adoption of the Joint Strategic Plan for Management of Great Lakes Fisheries (Anonymous 1981) is an important first step toward controlling that risk.

Peyton (1987) pointed out that optimum production and apportionment of Great Lakes resources would ultimately be defined largely by sociological considerations. Yet social wisdom is drastically outpaced by technological and economic capability (McFadden 1969). Affected and nonaffected segments of society influence the predictive capability of resource managers through the political process, by communicating priorities for resource management assessment and associated funding. To plan fisheries programs with a high degree of public acceptance, management agencies are faced with the problem of trying to evaluate a melange of individual beliefs and values that coalesce into a body of public opinion. Conflicts arise over public beliefs, values, and priorities. In addition, public support for resource management programs fails when confidence in the scientific basis for management is eroded. This erosion occurs when public segments are not fully involved in the planning and decision-making process and participate over a time period too short to allow the evolution of sound public value systems and priorities (Peyton 1987). Public priorities are too often based on belief systems that have been formulated without the benefit of exposure to all options, trade-offs, and long-term impacts. A body of public opinion, which is itself changing and unstable, places changeable short-term demands on Great Lakes fisheries resources. As this unstable mix of demands impacts resource management policies, it conflicts with the philosophy of a stable mix of species within the fish community.

Future Trends

In the preceding discussion we outlined the constraints on the generation and application of useful yield predictions. These constraints have biological, institutional, and societal origins. Despite these many difficulties, we believe increased efforts in a number of key areas can increase managers' predictive capabilities for Great Lakes fisheries.

First, in the area of yield prediction science, it has been made clear that data required to apply existing yield models are often inadequate. Continuing efforts are required to improve interagency communication to provide a basis for the standardization of data collection and analysis and the sharing of resources. Collection and integration of statistics on sport fishing catch and effort must be intensified. Continuing efforts to ensure high quality of commercial catch and effort data (including changes in gear efficiency) are also required. Reduced fishing mortality on lake trout stocks is essential, as is improved understanding of the impact of exotic salmonids. In many situations, however, existing models will be inadequate even with improved data. This symposium has indicated the need for further development of yield prediction science. New approaches incorporating climatic variables and interspecific interactions are required.

Second, there is a need for increased attention to conceiving and implementing progressive (not reactive) lake-wide management programs based on sound yield prediction methodology, with incorporation of socioeconomic factors. Consensus on desired fish communities is essential to the development of fisheries management plans. Single-species, joint-agency management (e.g. Lake Erie walleye, Lake Michigan ciscoes, and lake trout) has been successful because of agreement on goals for those species. A similar approach must be taken based on goals for fish communities.

Given the high degree of variability currently present in Great Lakes fisheries and the low resolution of currently available yield models, Walters (1987) and Milliman et al. (1987) maintained that yield prediction is not achievable for these systems in any practical sense of the word; the only option for effectively managing Great Lakes fisheries is to adopt an actively adaptive fisheries management system. This approach implies that fisheries agencies in the Great Lakes concentrate their efforts less on attempting to obtain data for use in yield models and more on developing flexible, responsive management systems. A comprehensive discussion of this approach was given by Milliman et al. (1987).

Although we agree that Great Lakes fisheries management systems must, by nature, be adaptive, we support the contention that a critical key to improved predictability of Great Lakes stocks is rehabilitation of the fish community, insofar as possible. Only through rehabilitation of Great Lakes fish communities can some degree of relative system stability be realized. The rehabilitation of fish communities would lay the foundation for less variable yields and therefore a higher degree of predictability. The present communities are rather poorly integrated systems that require large external inputs of unknown stability to produce fish flesh of value to humans. In contrast, rehabilitated, well-integrated systems can produce high-value

species, capable of withstanding indefinite harvesting by humans, within certain definable limits. This approach, securing fish communities based on self-sustaining stocks, is the primary goal of the Great Lakes Fishery Commission (Anonymous 1983).

Given the current state of knowledge, the rehabilitation process itself may be unpredictable in terms of fish communities. New approaches are needed to understand and measure progress toward the rehabilitation goal. Loftus et al. (1987) suggested using their yield partitioning forecasts as a benchmark for measuring progress toward rehabilitation.

Finally, the fundamental societal constraints on yield prediction must be addressed. Resolution of societal constraints is ultimately the key to resolving technological and institutional problems. Few management programs can be implemented without resolving issues presented by various segments of the public (Peyton 1987). Informed, rational judgments by representatives of society can lead to the political will to resolve the technological and institutional problems.

A sound public information policy that will form the basis for public value systems is needed. The public must be made aware of all the implications of Great Lakes management options, including an understanding of water quality, habitat, allocation, and stocking issues that pertain to all water users (including but not restricted to fish and fishermen). There is a need to identify and quantify objectively the various public segments with a stake in the management of a given resource. Market segmentation techniques may be an effective method for doing this (Peyton 1987). Involving the public in adaptive management workshops (Hilborn et al. 1984) can be beneficial. In these settings, groups and individuals can be exposed to the beliefs, values, and concerns of others and may modify their own positions. Regardless of the outcome, such settings provide exposure of groups and individuals to a range of concerns and values broader than their own, thereby facilitating a reassessment of value systems previously established. With respect to the application of yield prediction methodology, ensuring an informed public assists in securing necessary public support for critical components of the process: development of science, assessment programs, and management strategies (Peyton 1987).

Addressing constraints to effective yield prediction requires a more holistic systems perspective on the part of both the public and fisheries managers (Francis et al. 1979). Rehabilitation of Great Lakes fisheries, one key to improved predictability, must encompass ecological, social, economic, and political dimensions (Steedman and Regier 1987). Through increased public involvement in long-range goal-setting and strategic planning exercises, a public will may develop that can be translated into a political will to do what is necessary. Through increased public demand for critical assessment and research programs, coupled with a commitment to long-term resource stability rather than to short-term benefits, many of the biological, institutional, and societal factors currently constraining useful resource predictions on the Great Lakes can be overcome.

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Partitioning Potential Fish Yields from the Great Lakes[1]

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We proposed and implemented procedures for partitioning future fish yields from the Great Lakes into taxonomic components. These projections are intended as guidelines for Great Lakes resource managers and scientists. Attainment of projected yields depends on restoration of stable fish communities containing some large piscivores that will use prey efficiently, continuation of control of the sea lamprey (*Petromyzon marinus*), and restoration of high-quality fish habitat. Because Great Lakes fish communities were harmonic before their collapse, we used their historic yield properties as part of the basis for projecting potential yields of rehabilitated communities. This use is qualified, however, because of possible inaccuracies in the wholly commercial yield data, the presence now of greatly expanded sport fisheries that affect yield composition and magnitude, and some possibly irreversible changes since the 1950s in the various fish communities themselves. We predict that total yields from Lakes Superior, Huron, and Ontario will be increased through rehabilitation, while those from Lakes Michigan and Erie will decline. Salmonines and coregonines will dominate future yields from the upper lakes. The Lake Erie fishery will continue to yield mostly rainbow smelt (*Osmerus mordax*), but the relative importance of percids, especially of walleye (*Stizostedion vitreum vitreum*), will increase. In Lake Ontario, yields of salmonines will be increased. Managers will have to apply the most rigorous management strictures to major predator species.

Les auteurs appliquent des méthodes de division, en composantes taxonomiques, des rendements futurs des ressources piscicoles des Grands Lacs. Ces prévisions se veulent des lignes directrices destinées aux gestionnaires des ressources des Grands Lacs et aux scientifiques. La réalisation des rendements prévus dépend du rétablissement de communautés piscicoles stables composées d'un certain nombre de grands piscivores qui utiliseront efficacement les proies, de la lutte continue contre la lamproie marine (*Petromyzon marinus*) et de la reconstitution d'un habitat du poisson de haute qualité. Étant donné que les communautés piscicoles des Grands Lacs étaient en harmonie avant leur effondrement, les auteurs ont utilisé les caractéristiques du rendement historique comme composantes partielles pour la projection des rendements potentiels des communautés remises en état. Cette utilisation est faite sous toutes réserves à cause d'inexactitudes possibles dans les données qui ne portent que sur le rendement commercial, de l'existence d'une pêche sportive très développée qui influe sur la composition et l'importance du rendement et, depuis les années 1950, de modifications peut-être irréversibles des diverses communautés piscicoles. Les auteurs prédisent que les rendements totaux des lacs Supérieur, Huron et Ontario augmenteront suite au rétablissement tandis que ceux des lacs Michigan and Erié baisseront. Les salmonidés et les corégonidés constitueront la plus grande partie des rendements futurs des lacs supérieurs. Dans le lac Erié, la pêche continuera à générer surtout de l'éperlan arc-en-ciel (*Osmerus*

[1]Contribution 667 (Brown and Hartman), U.S. Fish and Wildlife Service, National Fisheries Center - Great Lakes, Ann Arbor, MI 48105, USA.

mordax) mais l'importance relative des percidés, surtout le doré jaune (*Stizostedion vitreum* vitreum) augmentera. Dans le lac Ontario, les rendements de salmonidés augmenteront aussi. Les gestionnaires devront appliquer les restrictions de gestion les plus rigoureuses aux principales espèces prédatrices.

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We describe the composition of early and recent fish yields from the Great Lakes and offer guidelines for partitioning potential fish yields from rehabilitated Great Lakes fish communities. Yield partitioning guidelines are useful because they identify targets for rehabilitation. They also serve as measures of what can be accomplished through rehabilitation in terms of improved quantity and quality of fish yield. Finally, they provide a context for discussions among scientists, managers, and public interest groups about rehabilitation strategies and objectives.

The collapse of Great Lakes fish communities due to the combined action of overexploitation, eutrophication, and the establishment of exotic species such as the sea lamprey (*Petromyzon marinus*) has been well documented (Loftus and Regier 1972). These communities are now dominated by smaller, less valuable species such as the rainbow smelt (*Osmerus mordax*) and alewife (*Alosa pseudoharengus*). They are also less stable and predictable than they were when large benthic species such as lake trout (*Salvelinus namaycush*), walleye (*Stizostedion vitreum vitreum*), burbot (*Lota lota*), and lake sturgeon (*Acipenser fulvescens*) predominated (Paloheimo and Regier 1982). Rehabilitation of Great Lakes fish communities is a primary goal of the Great Lakes Fishery Commission and of the individual government agencies involved. Basically, rehabilitation entails the restoration of stability, manageability, and high-quality fish yields to Great Lakes fish communities. Its basic elements include effective fishery regulation, restoration of fish habitat quality, continued effective sea lamprey control, and reestablishment of dominant populations of large piscivores, especially lake trout (Francis et al. 1979; Eshenroder et al. 1984). Strong arguments have been put forward suggesting that fish community rehabilitation can best be achieved by species native to the Great Lakes (Ryder et al. 1981; Ryder and Edwards 1985; W. J. Christie and K. H. Loftus, unpubl. data).

We assume here that the year 2020 is a reasonable target for complete rehabilitation of the fish communities of the Great Lakes. We believe that the following guidelines are appropriate for attainment of valuable yields of a multitude of species over a very long period.

An Approach to Yield Partitioning

There is an upper limit to the potential fish yield of a lake. This limit is related to morphometric and edaphic characteristics (Rawson 1952, 1955; Moyle 1956; Ryder 1965; Ryder et al. 1974) and to insolation (Ryder et al. 1974; Ryder 1982; Schlessinger and Regier 1982). Also, models of surplus production suggest that when fishing effort is already at a moderate or higher level of intensity, unit increases in fishing effort result in progressively smaller increases in equilibrium yield. This relationship applies to both single-species and multispecies fisheries. Therefore, average long-term yields from lakes where exploitation is moderately intensive can be used as estimates of potential yield (Ryder et al. 1974). This approach was applied to the Great Lakes by Ryder (1965) and Matuszek (1978) who used yield data from historical commercial fisheries to estimate the potential yield of each lake. Our approach was similar. We acknowledge, however, that true potential yields, such as those estimated by Leach et al. (1987), may be substantially higher than potential yield estimates based on historical yield data. The latter reflect the biasses and inefficiencies of fisheries in addition to lake productivity.

Sustained overexploitation results in declining yields in single-species fisheries and in changes in the composition of yields from multispecies fisheries (Regier and Loftus 1972; Larkin 1977; Pauly 1984). Changes in yield composition of overexploited multispecies fisheries are associated with the decline in abundance of larger, *k*-selected species (Larkin 1977) and with increases in abundance of smaller, less valuable species and unexpected increases in the abundance of previously insignificant species (Pauly 1984). There is a theoretical basis for expecting yields to increase as exploitation pressure shifts to fish species at lower trophic levels (Larkin 1977; Leach et al. 1987). This relationship may help to explain the relatively high yields of Lake Erie and Lake Michigan where rainbow smelt and alewives, respectively, have dominated commercial catches in recent years. This domination has not occurred in the other Great Lakes, however, and Paloheimo and Regier (1982) have suggested that yields from multispecies fisheries may, in fact, be independent of the trophic level of the species harvested. The data of Kerr and Martin (1970) and Goddard et al. (1987) tend to support this suggestion. This unresolved issue is a complex one, involving economic as well as ecologic factors.

Traditional fish stock assessment methods are generally inadequate for partitioning yields by species and species groups (Larkin 1977; Paloheimo and Regier 1982; Dickie et al. 1987). Gulland (1970), for example, suggested that in the absence of species yield data, total yields could be partitioned on the basis of mortality coefficients of constitutent species, an approach applied to tropical reservoir fisheries by Regier et al. (1971), Ryder and Henderson (1975), and Ryder (1978), but ill-suited for application to the Great Lakes. Alternative multispecies approaches, such as those offered by T. Laevastu and N. Bax (unpubl. data) and J. E. Beyer (unpubl. data), promise much greater short-term precision, but their demands for data constitute a major constraint on their application at the present time. A fundamental weakness of all such approaches is that their tendency to define fish species solely in terms of mortality, size, and type is inadequate to account for fish species interactions.

Observations of structural similarities in yield across boreal percid lakes by Adams and Olver (1977) led to a different and much simpler approach to yield partitioning. These investigators used Ryder's (1965) morphoedaphic index (MEI) regression model

$$\hat{Y} = 1.4(\text{MEI})^{0.45}$$

to obtain potential yield estimates ($\hat{Y}$, kilograms per hectare per year) for 70 northern Ontario lakes. They also devised the term

"relative yield intensity" (RYI), which is the average annual yield (Y, kilograms per hectare per year) expressed as a percentage of $\hat{Y}$. That is,

$$\text{RYI} = \frac{Y}{\hat{Y}} \cdot 100.$$

They observed that in lakes having RYI values of 50–100%, percid yields constituted 29–36% of the total yield (average = 32%) and about 20% of the potential yield irrespective of RYI, lake area, and lake productivity. They suggested, as did Kerr (1977), that this emergent characteristic of percid systems was a result of community organizational structures that promote homeostasis under exploitation. It followed that it was possible to partition potential yields by species (e.g. walleye) or by species group (e.g. percids).

A similar approach was taken by Strategic Program for Ontario Fisheries (SPOF) Working Group Number Twelve, which was established by the Ontario Ministry of Natural Resources (OMNR) to develop yield partitioning guidelines for the province's inland lakes (OMNR 1982). This group used creel survey and commercial catch data from 73 lakes, including 69 in Ontario. The fish species considered were lake trout, brook trout (*Salvelinus fontinalis*), lake whitefish (*Coregonus clupeaformis*), northern pike (*Essox lucius*), walleye, yellow perch (*Perca flavescens*), and smallmouth bass (*Micropterus dolomieui*). Yield guidelines were established for each species based on yield data from lakes where that species was actively sought. Tentative yield partitioning guidelines offered by OMNR (1982) and expressed as percentages of MEI potential yield estimates were as follows:

	Sport fisheries	Commercial fisheries
Brook trout	25	—
Lake trout	25	25
Lake whitefish	24	24
Northern pike	25	10–20
Smallmouth bass	17–50	—
Walleye	32	20
Yellow perch	13	—

Differences in the guidelines listed for sport and commercial fisheries were attributed to differences in method of capture and compensatory mechanisms.

The concept of harmonic fish communities (Ryder and Kerr 1978, and unpublished data) supports this approach to yield partitioning. Harmonic community theory was developed primarily on the basis of direct observations of fish behaviour, the comparison of fish community structure in different lakes, and the Hutchinson–Fry concept of the niche as an attribute of organisms rather than of their habitat (Kerr 1976, 1980; Kerr and Ryder 1977). It unifies three ecological paradigms: resource heterogeneity, time, and enemy impact (see Price 1984). It postulates that harmonic communities are integrated assemblages of coevolved species and that they are controlled by one or several dominant predators. They are thought to be efficient systems in terms of their use of available energy, materials, and space. Consequently, they are both resilient and productive. The species composition of yields from harmonic communities remains relatively stable, a conservatism that permits yield partitioning.

The relatively stable composition of fish yields from the Great Lakes before their collapse has been seen as strong evidence that the fish communities were harmonic (Ryder et al. 1981; Ryder and Edwards 1985; W. J. Christie and K. H. Loftus, unpublished data). It is therefore possible to use available species yield data from that period as a basis for setting guidelines for partitioning yields from rehabilitated Great Lakes fish communities.

To develop yield partitioning guidelines for the Great Lakes, one must take into account the changes, trends, and uncertainties that will affect rehabilitation programs and subsequent management of the reconstructed fish communities. Some general qualifiers in the application of yield partitioning guidelines are outlined in the report of SPOF Working Group Number Twelve (OMNR 1982). Those especially relevant to the present exercise are now discussed.

Historical Yield Data

Available historical yield data probably underestimate total fish yields. We have assumed that published historical yield data for the Great Lakes (Baldwin et al. 1979) reflected actual yields reasonably well, and also that the relative stability of individual species yields resulted from strong, homeostatic mechanisms within each community. We acknowledge, however, that the data are imperfect, for several categories of yield are not considered: unreported (unlanded) catches of fish that were spoiled or otherwise unmarketable; landings by commercial trollers and in native fisheries; and harvests by domestic and sport fisheries.

Also to be considered is the possibility that the stability of species yields before the collapse of the Great Lakes fish communities was more apparent than real. Fishing effort, as well as its effectiveness, tended to increase throughout the historical period. A progressive fishing-up process was in effect (Regier and Loftus 1972). Thus the abundance of preferred species may have declined even though species yields and total yields remained relatively constant. Langlois (1942) observed this in the collapse of the cisco (*Coregonus artedii*) in Lake Erie.

Great Lakes fish communities were probably severely stressed by overexploitation even before the expansion of sea lamprey populations caused the collapse of lake trout and burbot stocks. Lake sturgeon populations, for example, had been greatly reduced. The blue pike (*Stizostedion vitreum glaucum*) of Lake Erie was probably fished to extinction (Hartman 1973). Lake trout populations may have been severely stressed as well. The very rapid expansion of rainbow smelt populations in Lakes Michigan and Huron during the late 1930s, and of alewife populations in Lakes Michigan and Huron during the 1950s, may have taken place because depressed lake trout populations were then too small to control abundance of forage fish. Therefore, guidelines based on historical yield data must be cautious.

Changes in Fish Community Composition

Changes in the fish community composition of the Great Lakes have resulted from the loss of some endemic species and the establishment of exotics. Significant extinctions have included those of native lake trout from all of the lakes except Lake Superior, the disappearance of blue pike from Lake Erie, and the loss of Atlantic salmon (*Salmo salar*) and fourhorn sculpin (*Myoxocephalus quadricornis*) from Lake Ontario.

Numerous other endemic species populations have been so reduced so that their present roles are inconsequential. Lake sturgeon populations are a good example. Losses of the major predator species have had strong, destabilizing effects on all Great Lakes systems. The significance of other losses, such as those of lake sturgeon and fourhorn sculpin from Lake Ontario, are unclear. The fourhorn sculpin may have served as a primary agent for energy and materials cycling between profundal, pelagic, and littoral zones (Christie 1974).

Newly established species include alewife and smelt, sea lamprey, pink salmon (*Oncorhynchus gorbuscha*), white perch (*Morone americana*), rainbow trout (*Salmo gairdneri*), and common carp (*Cyprinus carpio*). Coho salmon (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) are also highly significant newcomers, but their numbers are maintained largely by artificial means. W. J. Christie and K. H. Loftus (unpubl. data) encouraged managers not to construe the presence of exotic species as an insurmountable obstacle in the rehabilitation process. For example, there is evidence that the high abundance attained by the alewife and rainbow smelt was more a result than a cause of the decline in abundance of lake trout (and walleyes, in Lake Erie) and that the reestablishment of large populations of piscivores will cause these species to decline, jut as alewife abundance fell dramatically in Lake Michigan after the stocking of Pacific salmons was intensified (Kitchell and Hewett 1987).

Smith (1972) believed that pink salmon had the potential to become the most abundant, naturally reproducing salmonine in the Great Lakes. Continuing rapid expansion of pink salmon populations throughout the lakes supports his view. Although its role in Great Lakes fish communities remains unclear, this species appears to have had no adverse effects (Ryder and Edwards 1985) and may make substantial contributions to fish yields in the future.

Much uncertainty surrounds the sea lamprey, the ability of managers to control its abundance, and the capacity of large lake trout populations to sustain themselves in its presence, with or without the lamprey control program.

Sport Fishery Development

Historically, the Great Lakes supported sport fisheries for a variety of species, including lake trout, walleye, blue pike, lake whitefish, yellow perch, lake herring, smallmouth bass, largemouth bass (*Micropterus salmoides*), northern pike, muskellunge (*Esox masquinongy*), brook trout, and panfish. However, these fisheries tended to be small and localized and the aggregate yields were probably relatively small. Loftus (1979), for example, estimated that at its peak in growth in the late 1930s the charterboat fishery for lake trout in the Canadian waters of Lake Huron may have harvested 100 000 kg. yr^{-1}.

Where friction between anglers and commercial fishermen has resulted in confrontation, commercial operators have had to give ground. An early example in Ontario was the creation in about 1913 of the "Georgian Bay Line" which excluded commercial fishermen from operating in the nearshore waters of eastern Georgian Bay.

Angling fisheries have expanded greatly in recent years as increasing numbers of people have acquired powerboats and plantings of salmonines have increased. Yields to angling may be substantial in some cases, such as the walleye fishery in western Lake Erie. The expansion of sport fisheries in the Great Lakes has placed new and increasing demands on managers to ensure good supplies of desirable fish species. Satisfaction among Lake Michigan anglers with the present, artificially maintained fishery for Pacific salmons has prompted managers in bordering states to consider maintenance of the status quo (the salmon–alewife system) as a primary management objective (Kitchell and Hewett 1987).

These trends are significant with respect to yield partitioning because sport fishermen are quite selective, relative to commercial fishermen, and because the latter are increasingly being displaced. Also, partitioning is relevant only to yields sustained by natural reproduction, and many of the present sport fisheries for salmonines are maintained by stocking. A large element of uncertainty is associated with predicting future yield partitioning because of the substantial resistance that may develop if managers wish to replace exotic salmon and trout with other species more appropriate for lake restoration (Francis et al. 1979).

Habitat Alteration

Alteration of fish habitat by eutrophication and other means has been cited as a possible cause of reduced species abundance and yields in the Great Lakes (Colby et al. 1972; Leach et al. 1977; Paloheimo and Regier 1982). Inshore areas, especially embayments and shallow areas, and tributaries have been greatly degraded or modified in the lower lakes, and further change throughout the Great Lakes basin is anticipated as the human population expands. Fish habitat rehabilitation is a necessary component of fisheries rehabilitation. Recent successes in reducing nutrients and other pollutants in areas such as Bay of Quinte (Minns et al. 1987) and Green Bay (Harris et al. 1982) are promising.

Contamination of fish by heavy metals, organic toxins, and other substances is a serious problem in the Great Lakes. It has resulted in temporary closures of some commercial fisheries and restrictions on fish consumption, as well as in direct effects on fish health.

Climate

Year-to-year variations in weather patterns and their impact on year class strength in fish (Christie and Regier 1973; Shuter et al. 1980) can cause pronounced changes in the absolute and relative abundance of fish species over time. Colby et al. (1987) observed weather-related changes in the relative abundance of smallmouth bass and walleyes. Extreme weather conditions also directly affect the adults of some species, such as the alewife (Colby 1973).

More important, however, from the standpoint of fish community composition and yield partitioning are long-term climatic trends such as those discussed by Cushing and Dickson (1976) and W. J. Christie and K. H. Loftus (unpubl. data). If scenarios predicting a rapid climatic warming due to increased atmospheric CO_2 concentrations (Pollard 1985) are correct, there may be large-scale changes in the distribution and abundance of fish species within the Great Lakes region.

Socioeconomic Considerations

The jurisdictional philosophies that influence how agencies choose to enhance, protect, and allocate surpluses from fishery resources will greatly affect future partitioning of yields. Current philosophies and the resulting management choices

have evolved in response to widespread ecological changes caused by overexploitation, eutrophication, and marine invaders and to socioeconomic issues raised by the tremendous growth of sport fishing since World War II (Smith 1968; Wells and McLain 1973; Hartman 1973).

Resource destruction by sea lamprey predation was so great throughout most of the Great Lakes in the 1950s that philosophical differences among agencies were put aside in a highly successful and continuing program of sea lamprey control, under the aegis of the International Great Lakes Fishery Commission. The various agencies and jurisdictions have generally continued this close cooperation in the integrated effort to attain self-sustaining lake trout populations and, despite some earlier differences and biological obstacles, recently endorsed comprehensive plans for lake trout rehabilitation in each lake. Unified management recommendations have also been developed since the early 1970s for the transboundary walleye population of western Lake Erie (Hatch et al. 1987) and stocks of bloaters (*Coregonus hoyi*) in Lake Michigan (Brown et al. 1985).

Problems in the allocation of resources among different user groups, intensified by the rapid post-war growth of the sport fisheries, have resulted in considerable divergences, however, among jurisdictional management policies. Some agencies have strongly emphasized sport fishery development because the economic returns to regional economies are greater than those from commercial fishing (Francis et al. 1979; Talhelm et al. 1979). The emergence of Indian fisheries in treaty-ceded waters of the state of Michigan in the late 1970s complicated resource allocation, but much progress has been made, including the signing of a court-approved negotiated settlement in 1985.

Lake Michigan is a graphic example of the complex interplay between the various ecological and socioeconomic changes and the ways that agencies have attempted to respond, and hence have influenced historical yields. Largely unregulated commercial fishing was the dominant exploitative force on the endemic fish community in that lake before the mid-twentieth century (Smith 1968; Wells and McLain 1973). Then, from about 1945 to 1965, sea lamprey predation was the dominant force, destroying or depleting stocks of valuable commercial species (lake trout and lake whitefish). Explosive increases in populations of invading alewives adversely affected various species in the 1960s and 1970s, and the introduction of Pacific salmon to control alewives stimulated the growth of an intensive recreational fishery for large salmonines. The salmon foraged heavily on alewives in "competition" with an industrial fishery that landed single-species tonnages (e.g. 22 000 t in 1977) that are records for the Great Lakes (Michigan Department of Natural Resources 1973; Baldwin et al. 1979). Lake whitefish populations recovered dramatically in the 1970s and yielded 1800 t or more in some years in the early 1980s to commercial fisheries, mainly in northern Lake Michigan (Baldwin et al. 1979; Great Lakes Fishery Laboratory, unpublished commercial fishery statistics). Bloaters and yellow perch underwent similar recoveries during a severe decline in alewife abundance in the early 1980s (Brown et al. 1985; Eck and Wells 1987).

Partitioning Great Lakes Fish Yields

To estimate future potential fish yields from the Great Lakes, we used average annual historical yields adjusted, where necessary, in consideration of the effects of changed limnological and fish community conditions on yields in recent years.

TABLE 1. Mean annual fish yield ($kg \cdot ha^{-1} \cdot yr^{-1}$) and percent of total yield for Lake Superior contributed by different species or species groups.

Species or species group	Early (1913–50)		Recent (1979–83)	
	Yield	Percent	Yield	Percent
Lake herring	0.651	66.4	0.139	36.6
Other ciscoes and chubs	0.018	1.8	0.041	10.8
Lake whitefish	0.048	4.9	0.080	21.1
Lake trout	0.240[a]	24.5	0.046	12.1
Rainbow smelt	0.000	0.0	0.041	10.8
Other species	0.021	2.1	0.028	7.4
Total	0.98		0.38	

[a]Based on the years 1920–45 only.

TABLE 2. Mean annual fish yield ($kg \cdot ha^{-1} \cdot yr^{-1}$) and percent of total yield for Lake Michigan contributed by different species or species groups.

Species or species group	Early (1920–50)		Recent (1979–83)	
	Yield	Percent	Yield	Percent
Alewife	0.000	0.0	1.684	61.2
Lake herring	0.341	19.8	<0.001	0.0
Other ciscoes and chubs	0.312	18.1	0.178	6.5
Lake whitefish	0.186	10.8	0.408	14.8
Lake trout	0.470[a]	27.3	0.019[b]	0.7
Rainbow smelt	0.076	4.4	0.215	7.8
Catostomods	0.137	8.0	0.108	3.9
Yellow perch	0.141	8.2	0.073	2.7
Other species	0.117	6.8	0.067	2.4
Total	1.78		2.75	

[a]Based on the years 1920–40 only.
[b]Includes lake trout backcross.

This approach was taken in preference to the use of less direct estimators such as those reviewed by Leach et al. (1987). Potential yield estimates were then partitioned among species and species groups on the basis of composition of historical and recent yields and on estimations of the structure of the rehabilitated fish communities of the future. The results are shown in Tables 1–5 in terms of yield (kilograms per hectare per year) and relative yield (percent total yield) and summarized in Table 6.

Early yields represent only the commercial catch derived from Baldwin et al. (1979) and are therefore subject to the caveats expressed in their table footnotes. We did not consider that the sport fish harvest would significantly alter the yield of any species or species group during this period. Recent yields were derived from the 1979–83 annual reports of the Great Lakes Fishery Commission. Because of the increasing sport fishery in recent years, available sport fish catches were added to the commercial catch, but these data have seldom been quantified.

Total early yields listed in Tables 1–5 are estimates of Great Lakes potential yields prior to the collapse of the fish communities. They are generally similar to those used by Ryder (1965) to develop the MEI model. Present yields are substantially lower than historical yields in Lakes Superior, Huron, and Ontario and higher in Lake Michigan and Lake Erie. In Lake Superior and

TABLE 3. Mean annual fish yield ($kg \cdot ha^{-1} \cdot yr^{-1}$) and percent of total yield for Lake Huron contributed by different species or species groups.

Species or species group	Early (1920–50)		Recent (1979–83)	
	Yield	Percent	Yield	Percent
Lake herring	0.269	20.1	0.004	7.1
Other ciscoes and chubs	0.066	4.9	0.044	7.9
Lake whitefish	0.210	15.7	0.245	43.8
Lake trout	0.387[a]	28.9	0.019[b]	3.4
Common carp	0.079	5.9	0.052	9.3
Catostomids	0.125	9.3	0.031	5.5
Ictalurids	0.015	1.1	0.048	8.6
Yellow perch	0.059	4.4	0.054	9.6
Sauger	0.003	0.2	0.001	0.0
Walleye	0.110	8.2	0.025	4.5
Other species	0.020	1.5	0.038	6.8
Total	1.34		0.56	

[a]Based on the years 1920–40 only.
[b]Includes lake trout backcross.

TABLE 4. Mean annual fish yield ($kg \cdot ha^{-1} \cdot yr^{-1}$) and percent of total yield for Lake Erie contributed by different species and species groups.

Species or species group	Early (1920–50)		Recent (1979–83)	
	Yield	Percent	Yield	Percent
Clupeids	0.000	0	0.156	2
Lake herring	1.042	14	<0.001	0
Lake whitefish	0.498	7	0.003	0
Rainbow smelt	0.000	0	5.380	56
Cyprinids	0.495	7	0.381	4
Catostomids	0.168	2	0.046	0
Ictalurids	0.142	2	0.084	1
Percichthyids	0.094	1	0.709	7
Yellow perch	1.099	15	2.031	21
Sauger	0.278	4	<0.001	0
Walleye	0.561	8	0.374	4
Blue pike	2.413	33	0.000	0
Freshwater drum	0.532	7	0.267	3
Other species	0.077	1	0.167	2
Total	7.40		9.60	

Lake Huron, the decline in total yield was due to the collapse of the lake herring and lake trout, species that have not yet recovered. In Lake Ontario, the stocks of lake herring, lake whitefish, Atlantic salmon, and lake trout collapsed, and available energy in the benthic and profundal zones has not been vectored efficiently into the remaining resources. The advent of a strong fishery for yellow perch has not restored total yield to historic levels. Lake herring and lake trout stocks were also decimated in Lake Michigan and bloaters declined. Lake whitefish harvests have increased, but the large increase in total yield in Lake Michigan in recent years was almost entirely due to the harvest of alewives. Despite the extinction of blue pike and the collapse of lake herring and lake whitefish in Lake Erie, total yield increased due to the harvest of rainbow smelt and (to a lesser extent) white bass and yellow perch. Western Lake Erie, which is shallow and warm and has been subjected to substantial

TABLE 5. Mean annual fish yield ($kg \cdot ha^{-1} \cdot yr^{-1}$) and percent of total yield for Lake Ontario contributed by different species and species groups.

Species or species group	Early (1920–50)		Recent (1979–83)	
	Yield	Percent	Yield	Percent
American eel	0.022	2.6	0.074	13.5
Lake herring	0.248[a]	28.8	0.003	0.5
Other ciscoes and chubs			0.000	0.0
Lake whitefish	0.229	26.6	0.002	0.4
Lake trout	0.122[b]	14.2	0.001	0.1
Rainbow smelt	0.000	0.0	0.017	3.1
Ictalurids	0.057	6.6	0.086	15.6
Centrarchids	0.003	0.3	0.047	8.5
Yellow perch	0.038	4.4	0.245	44.5
Other percids	0.041	4.8	0.009	7.5
Other species	0.102	11.9	0.066	12.0
Total	0.86		0.55	

[a]Early data published in Baldwin et al. (1979) combined catch data for lake herring and other ciscoes and chubs.
[b]Based on the years 1920–40 only.

cultural eutrophication over the past half century, very likely accounts for Lake Erie's extremely high recent yield.

A forecast of yield partitioning for the future, relative to the early and recent record, for each of the Great Lakes, is included in Table 6. Inasmuch as potential yield is based on natural reproduction, the hatchery component has been discounted, where applicable.

Historically, the upper Great Lakes were essentially salmonine–coregonine fish communities, and we expect these forms to be predominant again as rehabilitation is achieved. In Lake Superior, depressed lake herring stocks were recovering rapidly throughout the lake in the 1980s, and lake trout stocks will probably continue to increase, both species contributing to the attainment of historic harvest levels. Coregonines may attain early harvest levels in Lake Michigan; however, we predict that clupeids will not maintain their recent yield because of changing fisheries strategies and more efficient cropping by piscivores. We forecast that percid yields in Lake Huron will be similar to early yields and that total yield will increase slightly, compared with that in the past, as bloater stocks continue to rebuild. We do not expect that coregonine yields from Lake Erie will increase, unless rehabilitation is attempted through a major stocking program. The yield of rainbow smelt is likely to decline from its recent level as fisheries strategies change and as walleye stocks expand. Coregonine stocks in Lake Ontario will remain below historic levels unless chub (*Coregonus* spp.) stocks can be re-established. Lake Ontario salmonine yields may surpass historic levels as a result of the harvesting of a number of salmonine species by an intensive sport fishery. The yield of percids may also exceed historic levels. There is a measure of uncertainty associated with the rehabilitation prospects for Lake Ontario, which is reflected in the "other species" category in Table 6.

Management Implications

We have taken the optimistic view of Great Lakes fisheries rehabilitation: we believe it will be successful.

The yield partitioning guidelines offered here are tentative and subject to discussion and review. In general, they imply a

TABLE 6. Great Lakes fish yields ($kg \cdot ha^{-1} \cdot yr^{-1}$) and (in parentheses) relative yields (percent) by species group: early, recent (1979–83), and future (estimated for the year 2020).

Lake and period	Salmonines	Coregonines	Percids	Rainbow smelt	Alewife	Others	Total
Superior							
Early	0.24 (25)	0.72 (73)	—	—	—	0.02 (2)	0.98
Recent	0.05 (12)	0.26 (69)	—	0.04 (11)	—	0.03 (7)	0.38
Future	0.25 (27)	0.61 (65)	—	0.05 (5)	—	0.03 (3)	0.94
Michigan							
Early	0.47 (27)	0.84 (49)	0.14 (8)	0.08 (4)	—	0.25 (15)	1.72
Recent	0.02 (1)	0.59 (21)	0.07 (3)	0.22 (8)	1.68 (61)	0.18 (6)	2.76
Future	0.49 (30)	0.52 (32)	0.10 (6)	0.10 (6)	0.33 (20)	0.10 (6)	1.64
Huron							
Early	0.39 (31)	0.55 (44)	0.17 (14)	—	—	0.24 (19)	1.35
Recent	0.02 (3)	0.29 (52)	0.08 (14)	—	—	0.17 (30)	0.56
Future	0.55 (40)	0.51 (37)	0.18 (13)	0.02 (1)	—	0.11 (8)	1.36
Erie							
Early	—	1.54 (21)	4.35 (59)	—	—	1.51 (20)	7.40
Recent	—	0.00 (0)	2.41 (25)	5.38 (56)	0.16 (2)	1.65 (17)	9.60
Future	0.04 (0)	—	2.59 (35)	3.45 (46)	—	1.35 (18)	7.43
Ontario							
Early	0.12 (15)	0.48 (57)	0.08 (10)	—	—	0.18 (22)	0.86
Recent	—	0.01 (1)	0.25 (46)	0.02 (3)	—	0.27 (50)	0.55
Future	0.27 (31)	0.07 (8)	0.20 (22)	0.02 (2)	—	0.32 (37)[a]	0.88

[a]This includes an unassigned yield of 0.18 $kg \cdot ha^{-1} \cdot yr^{-1}$, or 20% of the total projected yield for Lake Ontario.

need for much larger stocks of terminal predator species than now exist and a reduction, through predation, in the abundance of prey species such as the alewife and rainbow smelt. The guidelines also leave managers with some latitude in terms of which species they manage and for what purposes. The Pacific salmons, for example, may continue to provide substantial recreational fisheries on the Great Lakes. We must agree, however, with the point made by Ryder et al. (1981) that Pacific salmons cannot be the only salmonines present in a rehabilitated fish community because they lack the niche potential necessary either to use fully the productive capacity of the lakes or to exert the general regulatory influence required. Thus they may serve better as supplements in communities dominated primarily by native lake trout. In some cases, it may even be necessary, for purely biological reasons, to use at least two salmonine predators.

At best, the rehabilitation of Great Lakes fish communities will result in greater community stability, improved quality of yields, and, in some, increased total yields. Extinctions of some endemic species and the presence of exotics preclude the possibility of regaining community harmony in the strict sense of the term, but the size and quality of yields specified by the yield partitioning guidelines are achievable.

Because fish community control (achievement and maintenance of restabilized communities) may be accomplished most easily by control of major terminal predators, these species should be subject to the most rigorous regulatory strictures. Management to achieve optimum production of terminal predators may require allocation of prey species to predator production, as a means of community maintenance, rather than to harvests.

Restoration of the quality of fish habitat is a fundamental aspect of fisheries rehabilitation in the Great Lakes. The use of biological indicators of ecosystem quality, such as those proposed by Ryder and Edwards (1985), should be further developed, as should the use of such community indicators as zooplankton mean size and forage fish abundance.

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Policy Making within an Adaptive Management Framework, with an Application to Lake Trout (*Salvelinus namaycush*) Management

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Using lake trout (*Salvelinus namaycush*) rehabilitation in the Laurentian Great Lakes as an example, we combine a policy design process known as "adaptive management" in biological circles with basic concepts found in natural resource economics. Emerging from this synthesis of biological and economic thought is a practical method for making policy choice in fisheries in the presence of biological uncertainty. We introduce this method by first reviewing key biotic uncertainties which impede the progress of lake trout rehabilitation. Drawing upon these uncertainties, a framework is proposed for developing a set of policy options. Included in these options are "actively adaptive" policies which are purposely experimental in hopes of both reviving the lake trout fishery and concurrently yielding data which may alleviate the nagging uncertainties. Using basic concepts from natural resource economics, we then outline how, in the presence of the key uncertainties, the policy which most likely maximizes socioeconomic gains can be chosen from the various options. We conclude with some brief policy implications for lake trout rehabilitation.

En utilisant comme exemple le rétablissement du touladi (*Salvelinus namaycush*) dans les Grands Lacs laurentiens, nous combinons un processus d'élaboration des politiques, connu sous le nom de «gestion adaptative» dans les milieux biologiques, avec les concepts fondamentaux de l'économie des ressources naturelles. De cette synthèse de la pensée biologique et économique émerge une méthode pratique permettant de faire des choix de politique dans le domaine des pêches en présence d'incertitudes sur le plan biologique. Nous présentons cette méthode en examinant tout d'abord les incertitudes biotiques clés qui empêchent le progrès du rétablissement du touladi. À partir de ces incertitudes, nous proposons un cadre pour l'élaboration d'une série de choix de politique. Parmi ces choix se trouvent des politiques «activement adaptatives», à caractère délibérément expérimental, qui devraient à la fois stimuler la pêche du touladi et fournir des données qui éclairciraient les incertitudes chroniques. À l'aide des concepts fondamentaux de l'économie des ressources naturelles, nous présentons le moyen de choisir parmi les diverses options, en présence des incertitudes clés, la politique qui a le plus de chance de maximiser les gains socio-économiques. La conclusion indique brièvement quelques orientations concernant le rétablissement du touladi.

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Effective fishery management requires socioeconomic as well as biological information (Pitcher and Hart 1982; Clark 1985). Biological predictions are necessary but not sufficient to indicate the most appropriate management action. Rather, the most appropriate action is determined by the degree to which a policy, via its biotic impact, advances important socioeconomic objectives, such as enhanced economic welfare, greater cultural opportunities, and species preservation. Unfortunately, effective policy choice is often hampered by key biological unknowns which impede accurate biological predictions; hence, the associated social and economic benefits are obscured as well. In this paper, we outline an approach for making policy choice under these conditions of uncertainty. The first part of the paper describes how the adaptive management framework can be used to construct a set of policy options available to managers; in the second part of the paper we illustrate how to choose the most appropriate policy

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option using socioeconomic as well as biological information. To focus the discussion, we apply the framework to lake trout (*Salvelinus namaycush*) rehabilitation in the Laurentian Great Lakes. Some tentative implications for lake trout rehabilitation are presented at the end of the paper. This paper does not attempt to integrate major strands of thought on fishery policy design as found within the fishery biology discipline. Rather, our synthesis occurs across disciplines. More specifically, we will integrate a policy design process found in fishery biology with concepts found in natural resource economics. We believe that this integration of biological and economic concepts will provide a useful framework for making policy choice in fisheries.

Policy Design for Lake Trout Rehabilitation: An Adaptive Management Approach

Prediction Uncertainties Associated with Lake Trout Rehabilitation

A number of viewpoints exist about the predictability of responses to lake trout rehabilitative measures such as stocking, harvest regulation, and sea lamprey (*Petromyzon marinus*) control. At one extreme is the viewpoint that a balanced and productive natural community can be reestablished if there is sufficient investment to reduce various stresses. At the opposite extreme is a viewpoint of nature chaotic, with violent and unpredictable future changes associated with factors ranging from predator–prey imbalances to exotic species introduction. Between the two extremes is a variety of viewpoints about the predictability of some phenomena (such as biomass size spectra or the dynamics of lake trout population recovery), tempered with the recognition that there are key gaps in understanding that make it impossible today to decide among various alternative hypotheses about long-term productivity and stability. This synthesis paper offers one viewpoint that has arisen through experience in trying to model the dynamics of lake trout recovery; this viewpoint stresses the need to precisely identify alternative predictions about future changes and to design adaptive management policies that will include adequate monitoring and the flexibility to change policy as it becomes clear which alternative prediction (if any) is correct. This viewpoint shares some similarities with a concept known as "experimental management," which also focuses on the design of management policies in the presence of biological uncertainties (Loftus 1976). This latter concept has been used by Ontario fishery researchers (K. Loftus, 130 Arnold Crescent, Richmond Hill, Ont. L4C 3R8).

As a result of the Sea Lamprey International Symposium (SLIS) the Great Lakes Fishery Commission (GLFC) subsequently sponsored a series of Adaptive Environmental Assessment and Management (AEAM) workshops that brought Great Lakes researchers and managers together to develop simulation models for predicting various fish community changes. Lake trout were emphasized in two of these workshops (Koonce et al. 1982; Jacobson et al. 1985), and a series of related models were developed to look particularly at stocking, lamprey control, fishery regulation, and the possible impact of changing prey fish resources due to the various introduced salmonids. At these workshops, biologists familiar with the historical and experimental data worked with modeling teams specializing in theoretical models of prey selection, growth energetics, and other processes. The simulation models produced in the workshops thus reflected a complex mixture of empirical experience with some biological processes (such as lamprey predation and survival rates of planted lake trout) along with pure speculation about others (such as switching by salmonids from feeding on alewives (*Alosa Pseudoharengus*) to feeding on native fish species). The modeling approach explicitly rejected both purely empirical prediction based on past experience (since the current fish community involves essentially novel processes and interactions) and purely theoretical predictions based on existing schools of thought about productivity and stability. In essence, the participants tried to do the best possible job in fitting experience with process theory, so as to make some dynamics predictions about the next 20–30 yr of lake trout population change.

The AEAM Lake Trout Workshops were to a degree a microcosm of the varying viewpoints expressed at ASPY, and in them the participants were unable to reach clear consensus about a single best prediction of lake trout population changes. Instead, the participants foresaw a series of possible futures which reflected the following key uncertainties:

(1) Lake trout recovery and sustainable exploitation rates will depend critically on the patterns of recolonization of historical spawning areas and the early survival rate (to yearling age) of eggs laid in these areas (Walters et al. 1980b).

(2) Maturity, fecundity, and vulnerability to various mortality agents depend strongly on body growth rates, and it is not clear how the growth pattern will change as the prey fish species composition shifts back toward a native mixture (Walters et al. 1980b).

(3) Lamprey predation on lake trout is presumably "buffered" by the presence of an assortment of alternative prey species, not all of which are currently exploited and monitored (e.g. burbot (*Lota lota*) and common white sucker (*Catostomus commersoni*)). There is no empirical (or theoretical) basis for predicting future changes in the abundance of such species and hence their capacity to absorb some lamprey attacks that would otherwise cause trout mortality (Walters et al. 1980b) (Walters et al. 1980a).

These uncertainties do not involve qualitative features of stressed versus natural ecosystems; rather they are quantitative differences in rate processes and hence trends in lake trout stock size over time.

The AEAM models present a general qualitative prediction about lake trout population equilibrium, namely that this equilibrium is a folded, or catastrophic, function of exploitation rates (Walters 1986). At low exploitation rates, stocks should recover (eventually) to high levels; at high exploitation rates, only a low, stocked fish based equilibrium should exist; at intermediate rates the wild stocks may move to either low or high levels depending on current abundance and may show rapid increases of catastrophic declines similar to the historical collapses. Depending on how seriously one takes simulation models, this is a frightening picture because it involves wildly divergent predictions which are generated by small changes in the quantitative parameter values that define the location of the catastrophic fold (exploitation rates at which collapse or recovery will begin). The location and depth of the fold, which is created by depensatory lamprey predation (increasing relative impact as trout stock decreases), depends on all three of the major uncertainties mentioned above.

The AEAM workshops were further unable to provide a scientific consensus about the future productivity and stability of a rehabilitated fish community containing a few exotica (such

as lamprey, which is probably impossible to eradicate) and missing some indigenous species/stocks that have been driven extinct. Using various plausible models for predator–prey and competitive interaction, the participants were able to produce predictions ranging from global stability to chaotic patterns of boom and bust among the smaller (salmonid prey) and littoral (walleye (*Stizostedion vitreum*), yellow perch (*Perca flavescens*), etc.) community components.

There are at least three ways to view the AEAM (and related) modeling results: (1) as incompetent modeling (i.e. it did not account for known properties of fish communities), (2) evidence that prediction is impossible, and attempts to do so are futile (i.e. we will not learn more about how the system works), or (3) as a clear indication that while no single prediction can be trusted, there is a well-bounded range of possible outcomes that can be compared with future monitoring data and used in the design of adaptive management policies. In the remainder of this section, we will adopt that last view and will discuss the process of adaptive policy design and evaluation which aim to provide the capability to respond (i.e. initiate new rehabilitative measures) as the outcomes of the grand rehabilitation "experiment" reveal themselves over the next two decades.

Elements of Adaptive Policy Design

Renewable resource management is generally practiced as an adaptive process in the sense that changing resource states are monitored and policies are altered over time as assessments provide evidence of undesirable trends or opportunities for development. However, it would be a grave mistake to view (or deliberately design) such adaptive processes as either blind, trial and error tinkering with management actions or as passive responses to disturbances over which the management system has no control or predictive capability. "Active" adaptive management should be a highly focussed, foresightful process in which the management system makes every effort to predict possible outcomes of its actions, attempts to detect (monitor) which outcome is occurring, and (within its range of policy flexibility) plans a response to the future threats or opportunities that each outcome represents. Within such a framework, disturbances and risky decision choices present opportunities to learn more about the system's response patterns. Major uncertainties, such as the three listed above for lake trout, are viewed not as research problems to be resolved through basic scientific investigation *prior* to management action, but rather as foci for monitoring activity. That point is crucial: major uncertainties in resource management often involve biological or physical processes that are only exhibited on large spatial and temporal scales (colonization of reefs, growth under free ranging feeding conditions, search and prey selection by lampreys) where controlled scientific experimentation is practically impossible or prohibitively costly.

The process of actively adaptive policy design involves at least four steps; each demands an attempt to make predictions based on current understanding while embracing the possibility that the predictions will fail:

(1) Construct predictive models (autecological, synecological, and/or intermediate versions) based on past experience and existing theory, and note the sensitivity of those models to parameters and relationships for which the data and theory do not provide definitive estimates.

(2) From the modeling exercise in (1), identify key uncertainties and represent these in terms of a range of alternative hypotheses about how the system could change over time.

(3) Based on the range of possible outcomes identified in (2), define a set of policy options ranging from conservative avoidance of risky actions to a more deliberate choice where alternative hypotheses predict quickly divergent responses.

(4) Construct a decision table in which the possible outcomes of each policy option is displayed, so that the policies can be compared in terms of robustness (i.e. whether there is a policy that should perform well no matter which hypothesis is correct) and in terms of formal decision theoretical measures such as expected value (if the hypotheses are assigned Bayesian probabilities or relative credibilities) (the use of a decision table for policy choice is discussed in the second section of the paper).

These four steps are not intended to provide a cookbook recipe from which an optimum policy will emerge at step (4); rather, they are intended to provide a framework for organizing the analysis of data and exploration of policy choices in a format that highlights (rather than hides) uncertainties and stimulates a search for imaginative policy options that can deal with a variety of possible future outcomes. In short, they are intended to engender a balance of emphasis between attempting to make biological predictions versus attempting to design policies that provide for healthy response and recovery in the event that the predictions fail.

There is a critical judgemental problem in moving from step (1) to steps (2) and (3) in the adaptive design process. Many assessment exercises and discussions never move beyond step (1); data and methods are at times massaged and applied endlessly in hopes that some breakthrough will occur to resolve the nagging uncertainties. The adaptive management approach is based on the presumption that it is wiser to be prepared for an incorrect prediction and to direct further work instead of how to best live with the uncertainty. It requires judgement to know when the scientific uncertainty makes adaptive policy design more attractive than passive policy design. The adaptive policy design process must itself be approached adaptively, recognizing that errors in judgement and wasted effort are likely to occur both in making predictions and in formulating policy options. Improvement of key parameter estimates is a very plausible outcome, but is not guaranteed; nor can researchers automatically assume that invalid models will always be discarded. Model predictive power may also vary with stock size and other fish community changes, i.e. one model may work best at low stock sizes, while another may predict well at higher abundance levels. This likelihood further complicates model design efforts found in step (1).

Making Policy Choice

Constructing the Decision Table

We now illustrate, with a simple example, how managers might make choices among the set of policy options developed from steps (1)–(3) of the previous section. Assume for simplicity that these steps have identified two policy options which might be applied to (say) the Lake Superior lake trout fishery:

(1) A "passively adaptive" policy, in which the major objective is to maintain large trout harvests; attaining large natural stocks is a secondary goal. Harvest and stocking rates are initially high under this policy. Using standard modeling techniques, managers make their "best guess" as to how the resource will evolve over time and do not extensively monitor stock movements for prediction purposes, choosing instead to

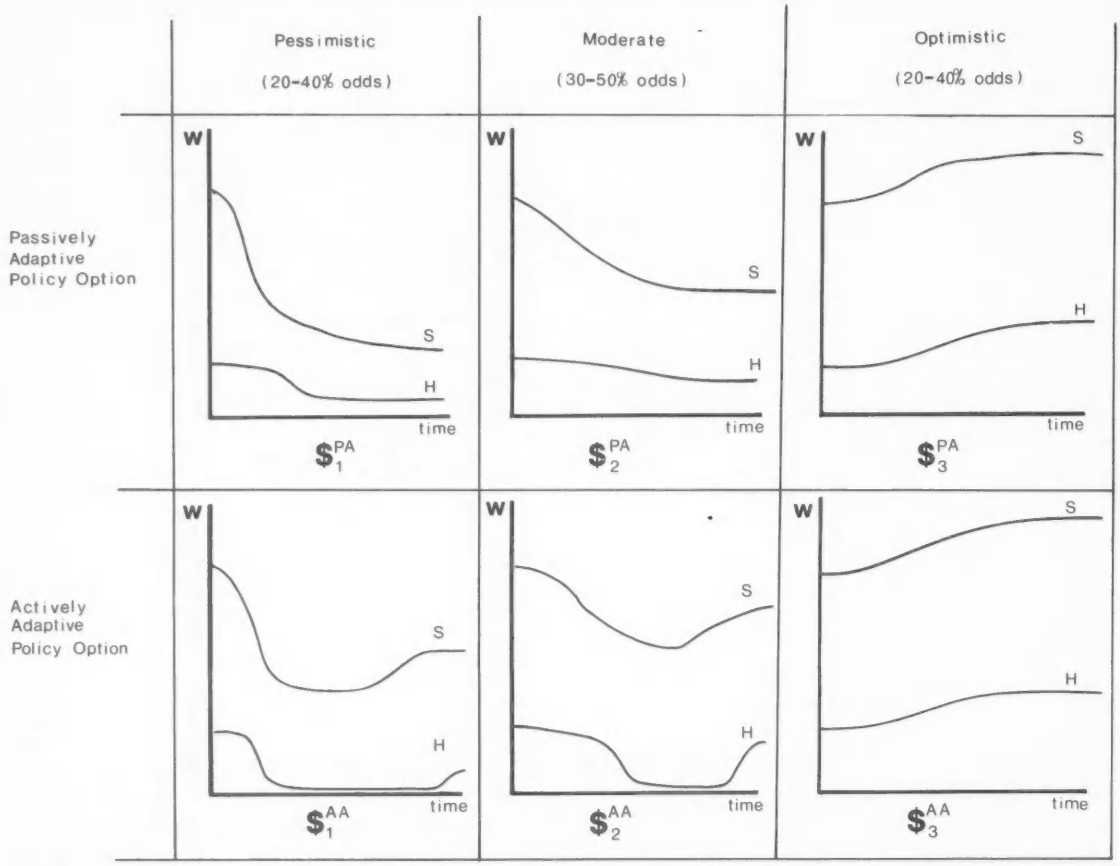

FIG. 1. Decision table which arrays the future biotic states across the top of the table (pessimistic, moderate, and optimistic) and the policy options down the left-hand side of the table (passively adaptive and actively adaptive). Probability ranges associated with each future biotic state are given in parentheses at the top of each column of the table. Each cell within the table represents a future biotic state – policy option combination. Contained in each cell is a graph detailing the expected qualitative changes in stock size (*S*) and harvest (*H*) over time in weight (*W*) for each combination. Below each graph within these cells are symbols ($) representing the net socioeconomic gains (positive or negative) associated with each combination, with subscripts on these symbols denoting the future biotic state (1 for pessimistic, 2 for moderate, and 3 for optimistic) and the superscripts denoting the policy option (PA for passively adaptive and AA for actively adaptive).

observe (and react) to the biotic outcomes which materialize. If natural stocks decline, then additional stocking is undertaken to maintain catch rates. Stocking costs are thus high (especially if natural stocks decline), but other regulatory costs (enforcement and biological monitoring) are low under this option. This policy option can be accompanied with the proviso that the extinction of natural stocks is to be ruled out, b· !·w to moderate natural stock levels are acceptable.

(2) An "actively adaptive" policy, in which the major goal is to attain large natural stocks; maintaining large trout harvests is a secondary goal. Harvest and stocking rates are again high initially, but managers now attempt to anticipate future biotic states via extensive monitoring. If severe natural stock declines are foreseen, then harvest controls are quickly imposed. Monitoring is continued with the twin goals of assessing the effectiveness of the controls and to collect valuable data on lake trout population dynamics which may aid future rehabilitation efforts. In addition to large stocking costs, this option entails high monitoring expenses and possible high enforcement costs as well (should harvest controls be imposed). Policy flexibility is paramount, since natural stocks may decline quickly if the appropriate actions are not taken.

Drawing upon the key biological uncertainties identified in step (2), assume that the following future biotic states have been identified by the Lake Superior managers: "optimistic," in which reef recolonization is extensive, egg survival is high, body growth rates are normal, and lamprey predation is low to moderate due to effective buffering by alternative prey species; "moderate," in which egg survival is high and body growth rates are normal, but lampreys greatly reduce reef recolonization progress (and thus egg deposition) via predation on older, sexually mature adults; "pessimistic," in which low to moderate egg survival and below-normal body growth rates are combined with moderate to high lamprey predation, which (depending on the harvest level) could send natural stocks reeling toward collapse.

Finally, assume that steps (1)–(3) have also enabled biologists to assign plausible probability ranges associated with the

three biotic states listed above, i.e. the optimistic state has a 20–40% chance of occurring, the moderate state a 30–50% chance, and the pessimistic state a 20–40% chance.

A "decision table" in Fig. 1 organizes these results, with columns representing future biotic states and rows representing policy options. Within the cells of the decision table are both the resulting stock and harvest movements *and* the associated economic impacts:

(1) The graphs within the cells illustrate time paths for lake trout stock size (S) and harvests (H), respectively (with time on the horizontal axis and W denoting weight on the vertical axis).

(2) Under each graph within the cells are the associated socioeconomic "net benefits" (measured in dollar terms) which are discussed in greater detail shortly. These impacts are presented by the $ terms, with the superscript denoting the relevant policy option (PA for passively adaptive and AA for actively adaptive) and the 1, 2, and 3 subscripts representing the pessimistic, moderate, and optimistic future biotic states, respectively. Listed at the top of each column are the probability ranges associated with the three possible biotic states.

Estimating Net Social and Economic Benefits

For each biotic state – policy combination, economists would attempt to measure social welfare changes (in dollar values) over time for consumers of commercially caught fish (consumer surplus), commercial fishers and wholesalers (producer surplus), sport anglers (another form of consumer surplus), and "existence" values for society at large due to preserving an ecosystem and/or species (the contingency value of knowing that a species/ecosystem exists; it is unrelated to direct fish consumption).

Measuring such values is not easy; in particular, estimating welfare impacts for sport anglers and nonconsumptive users (existence values) is difficult. Economists and other social scientists would also be concerned about broader concerns, such as changes in income distribution, fostering/protecting important cultural traditions, enhancing democratic ideals and institutions, and increasing economic opportunities (e.g. employment) for disadvantaged members of society or economically depressed areas.

These latter concerns often cannot be easily quantified and so are usually weighted subjectively in the analysis (if required). Sometimes a certain objective is so highly valued that we might impose the constraint that policies which violate this objective are to be discarded, e.g. policies which violate recognized Indian treaty rights might be dropped from consideration.

Proper Discount Rate and Time Horizon

Each biotic state – policy combination generates a stream of net economic benefits (benefits minus costs) over time. In order to compare streams across policies, we need to express net benefits figures in "present value terms," i.e. we must take into account the fact that, after controlling for inflation, a dollar of net benefits which occur at different points in time do not have the same value in the current time period (Clark 1985). Economists utilize a "social discount rate" to express society's time preference for net benefits: a high discount rate (say 10%) places a smaller value on future benefits and costs relative to a low discount rate (2%). The discount rate chosen has a marked impact on the analysis. A low discount rate, for example, tends to place significant weight on economic net benefits up to 30–40 yr into the future; thus, lake trout restoration schemes which increase the long-term catch may look attractive. A high discount rate, however, tends to reduce considerably any economic benefits/costs beyond 12–15 yr; thus, the benefits from far-term harvest increases would receive little weight. A consensus among economists concerning the "proper discount rate" for evaluating policy changes does not exist, but most would probably favor a discount rate somewhere in the range of 4–10% (cogent arguments for a lower rate, however, do exist). It is important to conduct a sensitivity analysis for a range of discount rates. We emphasize that the discount rate (as we are now discussing it) reflects people's differing preferences for valuing current versus future economic benefits. We are assuming that these benefits have already been corrected for inflation.

A related issue is: How far into the future does the analyst measure net social and economic benefits from a policy change, i.e. what is the proper "time horizon?" Theoretically the answer is that the time horizon should be long enough to encompass all welfare impacts from a given policy change. In practice, however, it is difficult to pinpoint the life of these impacts; thus, analysts may have to utilize several plausible time horizons and conduct a sensitivity analysis. As noted above, with a moderate to high discount rate, the time horizon is of less consequence, since far-term benefits and costs are discounted heavily; but with a low discount rate, such a result will not necessarily hold. Other things being equal, the economic benefits of fishery restoration plans which generate long-term harvest increases are greater with a long time horizon and a low discount rate. Readers can find a more detailed discussion of these economic concepts in Sugden and Williams (1978).

Making Policy Choice

The "best" policy might be chosen from the decision table by calculating the expected value (EV) associated with each policy option. This is done by multiplying, for each option (AA or PA), the expected odds of occurrence (P_i) times the associated net economic benefit:

$$(1) \quad \mathrm{EV} = \sum_{i=1} P_i \cdot \$_i^{\mathrm{AA\ or\ PA}}.$$

The policy option which yields the highest expected return could then be judged "optimal." However, some qualifications are in order. If decision-makers (and user groups) are "risk neutral" with respect to large benefit changes, then the expected value criterion will pinpoint the "optimal" policy. In fact, however, managers and user groups may be risk averse; thus, expected return calculations may not yield the most appropriate policy, i.e. the benefits from riskier policies would be overstated relative to less risky policies. Managers would have the information to correct for this bias by considering the question: How much in additional expected benefits must the riskier policy option generate in order to be ranked equally with the less risky policy? If such additional benefits do exist, then the riskier policy might be judged more appropriate.

Policy Implications: Making Lake Trout Rehabilitation Look Economically Attractive

Managers might want to think about the following issues:

(1) Advocates of lake trout restoration programs which require user groups to wait 10 or more yr before significant harvest increases materialize may want to favour a low discount rate;

otherwise an economic analysis of these programs may generate a negative net benefit figure (of course, the use of a low discount rate, even if justified, will not guarantee positive net economic benefit).

(2) It is very likely that sustainable trout harvests from natural stocks will be no larger than harvests from stocked populations and in fact could be substantially smaller. If so, then rehabilitation advocates may want to argue that (a) increased natural reproduction will result in large cost savings from reduced stocking which in turn will outweigh losses from reduced harvests and/or (b) substantial "existence" values are generated by large, naturally reproducing stocks, which in turn would be severely reduced if natural stocks fell to smaller sizes.

(3) Alternatives to rehabilitation may demand management efforts in perpetuity; these efforts may have to be maintained even when circumstances change drastically, e.g. the planting of Pacific salmon to meet angler demands in the face of the collapse in forage species.

(4) Naturally reproducing lake trout stocks may be useful to managers as reliable indicators of overall ecosystem health (Ryder and Edwards 1985). Of course, lake trout may not be the only species which could perform this role.

(5) Lake trout management cannot always be divorced from several broader policy issues, such as water quality. For example, the actively adaptive policy option discussed earlier may be inoperable unless, in the future, additional money is allocated towards water clean-up. When this integration of policy issues occurs, our framework for making policy choice must be expanded to include all the relevant benefits and costs associated with fishery management actions, e.g. water clean-up costs must be considered under the actively adaptive policy option. To keep our analysis simple in this paper, we have placed aside this consideration; but such a step would be highly unwise when making actual policy.

Some Final Thoughts

Fishery policy development is an imprecise art which is subject to uncertainty and surprises. The adaptive management approach, by attempting as much as possible to anticipate (and thus highlight) these possibilities, may enhance policy effectiveness. Various steps of this approach are of course difficult to carry out precisely. For example, highly accurate, specific estimates of net economic impacts are probably unattainable for many policy options. However, reasonable "guesstimates" may be all that is required to make effective policy choice in many settings. As the efficacy of biological monitoring instruments improves, so might the workability of various actively adaptive management plans. The viability of these latter policies in the political arena may also grow as the affected user groups receive increased exposure to them.

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Problems Associated with Fisheries Assessment Methods in the Great Lakes

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This paper presents a review of Great Lakes fishery assessment problems and addresses the variety of fisheries, the special circumstances created by rehabilitation, the emergence of joint strategic planning among fishery agencies, and convergence of water quality and fishery management. The inferences that emerge are that (1) continuing observation series are essential, (2) the variety of needs calls for a variety of assessment approaches, and (3) assessment objectives need to be clearly defined in order to protect the ongoing monitoring series. It is suggested that more attention should be given to fish community monitoring, to sport fishery statistics, and to gear calibration. On the other hand, improved coordination of human and material resources and focus on integration of water quality and fisheries assessment can achieve much, without great funding increases.

Notre étude passe en revue les problèmes d'évaluation des pêches dans les Grands Lacs et traite de la variété des pêches, des conditions particulières causées par les mesures de rétablissement, de l'apparition d'une planification stratégique conjointe parmi les organismes de gestion des pêches, et de la convergence de la qualité de l'eau et de la gestion des pêches. Nous en tirons les observations suivantes: a) il est indispensable de posséder des séries d'observations continues, b) la variété des besoins appelle une variété dans les approches de l'évaluation et c) il est nécessaire de définir clairement les objectifs de l'évaluation pour protéger les séries d'observations encours. Nous suggérons d'accorder davantage d'attention à la surveillance des communautés de poissons, aux statistiques sur la pêche sportive et à l'étalonnage des engins. Par ailleurs, il est possible d' améliorer la coordination des ressources humaines et matérielles et de mettre l'accent sur l'intégration de l'évaluation de la qualité de l'eau et des pêches sans grande augmentation du financement.

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The Great Lakes of North America are vast ecosystems that have undergone dramatic changes due to overexploitation, introduction of exotic species, and various other factors of cultural origin. Regulatory agencies, responsible for programs to maximize public benefits from the waters, are essentially obliged to proceed on the basis that steady-state communities with desirable fish species will be achieved within a realistically short time. Nevertheless, concern exists about whether assessment of the system changes will be adequate to meet the increasing and evolving needs of management.

Classical ecological theory and fisheries science methodology are limited as foundations for managing the Great Lakes ecosystems. This is true, in part, because of the complexity of the fisheries where the size varies from large vessel fleets through to diffuse nearshore operations and various sport fisheries. In contrast with the offshore marine fisheries which essentially can be separated on spatial grounds (May 1984), species and area overlaps require special attention in the Great Lakes.

Recently, fisheries assessment has been complicated greatly by dramatic recoveries of certain species from severe historical degradation documented in the Symposium on Salmonid Communities in Oligotrophic Lakes (SCOL) (Loftus and Regier 1972). Changes in regulatory controls, shifts in abundance of

commercial species, and emergence of native fisheries have produced many allocation disputes. This has led often to unrealistic demands for precise estimates of stock status and allowable catch.

Great Lakes fisheries assessment has also been impacted by increased interaction between jurisdictions with respect to both water quality and fishery management. Limnology and water quality management have moved towards increasingly intimate association with fishery science and fishery management. Also, the need for holism has been recognized in the adoption of the "ecosystem approach" in the 1978 U.S. – Canada Agreement on Water Quality and in the 1981 Strategic Great Lakes Fishery Management Plan (Christie et al. 1986). These advances signal the need for community assessment, which links spatially different parts of the same lakes and different parts of the food webs. Community assessment raises many problems about what and how to sample, how to convert from past procedure, and how to do so within currently constrained funding.

The ASPY case histories illustrate the variety of approaches used to deal with Great Lakes fisheries assessment problems. A purpose of this paper is to document the scope and intricacy of these problems. This is necessary because assessment is shifting perforce from a research orientation, where individual solutions to methodological problems were sufficient, to an organizational focus, where standardized approaches are required. New information needs are discussed and the opportunities to meet these needs, with extant methodologies or adaptations of new technologies, are reviewed. The generalities associated with setting assessment policy and priorities are discussed.

Dedication

For his significant and lasting contribution to this subject, we dedicate this paper to the late Ralph Hile (1904–1983).

Fisheries Problems

Measurement of Catch

Commercial fishery catches were compiled from reports submitted by commercial fishermen, as a condition of license, and the collection and reporting of the statistics have been standardized between the various Great Lakes jurisdictions (Baldwin and Saalfeld 1962; Baldwin et al. 1979). Although the overall quality is acceptable, the difference in the size of the fisheries probably introduces the largest source of bias, seasonal operators being less likely to produce good records than full-time professionals.

Management agencies of the Great Lakes have moved recently to regulation of the commercial fisheries by catch quotas, thus requiring immediate data about accumulated catches, in contrast with the former system in which fishermen's reports were collated months later. Logically, a quota system makes it profitable to falsify reports and assessment costs associated with ensuring accuracy have increased. On the Canadian side of Lake Erie, a port observer system has been developed recently where returning vessels must report for daily inspection of catches. This system works well for a large commercial fishery, but is not useful for the more diffuse fisheries elsewhere in the Great Lakes. Various approaches to regulation are used, including requirements for the preparation of daily catch reports, frequent inspection by enforcement officers, and heavy fines for falsification of reports. Competition between fishermen is leading to industrial self-regulation at the larger ports, but enforcement costs will remain high in the smaller, diffuse fisheries until self-policing is proven to be feasible.

Estimation of sport fishery catches is the most important single problem area: catches can seldom be tallied directly and are extrapolated from samples obtained by various survey techniques. This is expensive, however, and greater reliance has been placed recently on mail and telephone surveys to estimate catch. While these methods have become increasingly accurate and sophisticated, the results are of greatest value in measuring general public benefits, rather than specific parameters required for fishery models. Further developments may improve these data, but it is a clear deficiency that intensity of approach and design varies widely among jurisdictions. Substantial coordination is needed to develop coherent and reliable catch estimates on a system-wide basis.

Illegal fishing can produce large underestimates of total harvest. This problem is acute in the Great Lakes because many species spawn in small tributaries, where concentrations of fish are especially vulnerable to poaching.

Similiarly, there are significant problems with unreported, illegal by-catch of sport fish in commercial fisheries, and organized illicit trade still exists in some areas. There has, however, been a marked improvement in interjurisdictional cooperation in detection and action to suppress organized illegal catches, but the small diffuse activities remain poorly understood and only partly controlled. Improved education and communications will contribute to the longer-range solutions, but the short-term imperative is to develop enforcement-linked assessment to estimate accurately the illegal catches.

Measurement of Fishing Effort and Relative Abundance

Reporting of commercial fishing effort was introduced in the United States during the 1930's and became routine in Canada after 1948. Hile and Duden (1933) described the collection of statistics and Hile (1962) developed standards for calibrating effort units. These relative fishing power estimates have not been updated to account for subsequent fishing efficiency increases and the development of the trawler fishery.

Commercial catch statistics are typically more reliable than effort data because they are based on sales records, rather than on the fisherman's memory.

The kind of commercial fishery affects the usefulness of the effort data. Nearshore fyke net and trap net fisheries are licensed on an areal basis. Their constant unit optimization of effort assures that catch-per-unit-effort (CPUE) is a correlate of catch and, therefore, a true reflection of relative abundance. By contrast, data from set-line or gillnet fisheries often do not represent effective effort measures because the frequency of line or net landing varies with fish abundance and may vary with market conditions.

Effort measurement is critical also to the assessment of recreational fisheries. Expertise, and therefore effective effort, ranges from children and novice anglers to charter boat operators. The efforts of these extremes maybe assumed to be inconsequential, compared with the mean skill level. From the fish community perspective, this assumption may not be valid.

The use of catch and effort data to estimate relative stock abundance depends on the assumption that the effectiveness of effort units is affected only by random error in measurement, or by environmental conditions affecting the fishing success.

Systematic shifts in catchability, however, are commonplace. In the commercial fisheries, major gear improvements, such as the introduction of deepwater trap nets (Van Oosten et al. 1946) or the change from linen and cotton to nylon gill nets (Collins 1979), have been evaluated to interpret effort statistics. On the other hand, industry continually improves efficiency, resulting in subtle changes through time, which must be accounted for if species abundance is to be described accurately. Related to this is the observation that changes in the populations of commercial fishermen can also introduce serious shifts in the catchability coefficients (Christie et al. 1987). Similarly, Shuter et al. (1987) quantified the systematic shift in the average angling skill level, which biased significantly the estimates of relative abundance of a lake trout (*Salvelinus namaycush*) stock.

The areal component of the effort data also impacts the precision of abundance estimates. Historically, statistical zones for commercial fishing were set according to political boundaries and enclosed very large areas to minimize reporting error. This masked sequential fishing-up of stocks within zones (Lawrie and Rahrer 1973; Hile et al. 1951a) and forestalled preventative actions. Additionally, this effect confounds the application of both surplus yield and dynamic pool models for quota-setting purposes. Finally, as fishery agencies move towards joint strategic management plans, the need for information about shared or ecologically linked fish resources is increasing and large reporting areas obscure the resolution of pelagic and migratory stock data.

The importance of this problem was generally recognized by the 1970's, and since then, commercial fishermen have generally been required to provide more detailed catch location information, on the assumption that misinformation related to mistakes among small grids will be of minor importance compared with the large-scale effects. This fine-tuned catch and effort information, however, has not yet entered the interagency collation system. This is an urgent contemporary need in joint strategic planning, as well as in modelling and stock analysis.

Hile (1962) flagged the problem of identification of effort associated with by-catches and suggested an arbitrary effort classification system. The problem of effective effort has particular importance in the sport fisheries, where methods and gear can change quickly to redirect effort. A system such as Hile's is necessary as a standard for effort measurement.

In summary, systematic evaluations of fishing effort and other characteristics affecting catchability should be conducted routinely.

Variance-Related Issues

Hile (1954) discussed the significance of high natural variability in abundance of Great Lakes fish stocks to the application of the high seas management models. He stressed the importance of species interactions, especially in relation to the normal assumption of constant natural mortality. Subsequent analyses of the sequential degradations of fish communities led Christie (1974) to infer that recruitment levels often change systematically in response to stresses other than or in addition to overfishing. There is also variability in some environmental parameters relevant to assessment and management of Great Lakes stocks. These problems have in some cases obviated the application of the established steady-state models and in almost all cases have required modifications to suit Great Lakes situations.

Concurrently, fisheries managers are recognizing a need to develop assessment among regulatory agencies, which produces shared fish community understanding, within a broader ecosystem context. Invertebrate sampling can be carried out at frequencies related to the rates of change in abundance of organisms in lower trophic levels. Variations in fish abundance and availability have high amplitude, but much lower frequency. Sampling to address these scale differences is a major difficulty in understanding dynamic food web linkages.

High natural ecosystem variability and large-scale systematic changes are linked because both are inconsistent with steady-state assumptions. Periods of even relative system stability are difficult to identify using standard autecological descriptors, such that trends have usually been identified a posteriori. Community measures are not so labile. From the scientific perspective, therefore, it seems clear that predictive ecology will have to be developed along synecological lines.

The variability in freshwater fish stock abundance is associated with weather effects in several species (Christie 1963; Busch et al. 1975; Shuter et al. 1980). Correlations between climatic conditions associated with reproduction and early life stages and subsequent recruitment to the fisheries suggest relatively constant mortality levels during these periods. It is important to note that correlations between adult mortality and fishing effort have been demonstrated in such species as lake whitefish (*Coregonus clupeaformis*), walleye (*Stizostedion vitreum vitreum*), and smallmouth bass (*Micropterus dolomieui*). The inference is that conventional fishery models, which assume constant natural mortality, are suitable for terminal predators, while those species subjected to fish predation alone, or in combination with fishing pressure, require models which incorporate the varying effect of predation. This suggests that diet studies should become routine components of assessment.

Sample size requisites present special problems. The pivotal estimate for nearly all ecological or management studies is relative abundance, which is difficult to assess accurately. Green (1979) stated that "the number of samples required to achieve a desired level of precision is independent of the mean density and is approximately equal to the inverse of the square of the desired precision." In small bays, however, sample size requisites for assessment netting can often be met only by altering fish stocks. On the other hand, the size of the fishery can also limit the data volume. In the commercial fisheries, the samples from the reports or dockside interviews are limited by the number of fishermen or number of net lifts. Further, assessment netting has limits, as it is seldom possible to increase the effort to levels like those of the fisheries. This is because of budget limits and because of the normally accepted rule that such sampling should not affect the populations.

The characteristics of fishing success statistics differ greatly between fisheries and are influenced by fish behaviour and the variability of random catchability, such that variances often equal or exceed the mean values. This feature, combined with seasonal trends in availability or catchability of fish, dictates that confidence in a seasonal average CPUE must depend on the central limits theorem. Such data, therefore, are difficult to compare statistically in the short term and are only truly useful in extended time series. This consideration places a great deal of emphasis on rigorously systematic sampling, extended indefinitely through time.

Methodological Needs

Successes with Great Lakes rehabilitation have produced large institutionalized assessment programs, distancing them

from the small, diffuse research programs which constituted their origins. Consequently, many of the critical problems associated with small fishery assessment are even less likely to be tackled now during the present era of heavy workloads and constrained budgets. Moreover, these problems now assume vital significance in relation to strategic planning and multi-species management. In the following, continuing information needs have been distinguished from those which are more relevant to the emerging information needs.

Calibration of Catch and Effort Data

Hilde (1949) and Hile et al. (1951a, 1951b) illustrated the calibration of fishing power for different gears used to catch lake trout. In spite of this good background, only catch data are published on an international basis for all major species, lakes, and years. Hile's methods for calibrating effort statistics from the various jurisdictions to produce broadly applicable measures of fishing effort and to compute relative abundance measures have not come into common use, in spite of well-demonstrated needs.

The need for calibration of catch and effort data remains great because of the increased demands for more accurate population estimates in the current atmosphere of allocative disputes. Despite their complexity, commercial catch and effort statistics have proven their worth repeatedly in estimating relative abundance of various fish stocks and remain very important data sources.

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There is a clear need for assessment to account for changes in the nature of fisheries. Modern computing systems make it possible to calculate statistics for each fisherman and stabilize the averages for the changes in fishing behaviour or skill level. The termination of a commercial fishery ends the flow of relatively inexpensively obtained information about stock abundance and demands new measures, as well as the calibration to link with the earlier data. Equally, wholesale changes in seasons or areas fished can leave insufficient overlap to calibrate the new data with the existing series. This should be considered when regulatory or other changes are contemplated.

When new methods or technologies are adopted into a fishery, new efficiency equilibria are achieved quickly. The adoption of new technology, however, can be protracted according to economic circumstances or the practices of individual fishermen. For example, the use of monofilament nylon gill nets is legal in some parts of the Great Lakes, but some fishermen believe they are best used in combination with multifilament nets (Collins 1987). Fishermen are constantly experimenting. Some of these efforts succeed, leading in time to a general upgrading of efficiency in the fleets. With gill nets, the colour of the netting, the slackness of the netting as attached to the sidelines, the thickness, elasticity, and even fibre bonding of the thread are all under constant variation and experiment. Christie (1978) showed a striking difference in the selection properties of whitefish gill nets, which differed only in respect to the vertical length of the meshes, created by different net hanging methods. These practical experiments probably tend to converge effort efficiency, but at any given time, it is clear that catchability can be highly variable. Annual inventories of gear used by each fisherman should be an essential component of assessment.

Smaller-scale fishermen often contribute modestly to the aggregate catch, but can produce significant bias in the relative abundance statistics. Often their effort is more restricted locally (typically close to shore), and by using fewer or smaller units of gear, located precisely in time or space relative to fish concentrations, their CPUE's are often higher than the fleet averages. The large operations, by contrast, have better mobility and versatility, so that when fish availability declines, their effort is the first to be deflected to other species and areas. Unweighted CPUE statistics, therefore, will not accurately reflect stock abundance. Analytical approaches will improve the representativeness of the routinely collected statistics and can allow for real-time understanding of the magnitude of change in catchability.

Further refinements in the statistics of commercial catch and fishing effort are possible. Where gillnet fishing effort is correlated with fish abundance and intensive at the upper levels, the efficiency of mesh selection can be reduced from the eumetric norm towards the cacometric extreme (Beverton and Holt 1957). This exaggerates the variations in relative abundance in a trendless series and underestimates the catchability coefficient, when mortality and fishing effort are compared. Paloheimo and Regier (1982) offered a computational approach to dealing with this problem. The production of the mesh selection curves necessary for this approach has been an important contribution of assessment netting, involving the use of graded mesh gillnet series (McCombie and Fry 1960; Berst 1961). Many species have not been studied, however, and differences in the characteristics of the netting often call for the development of new selection curves, even for the same species.

It is conventional wisdom that the fishing mortality resulting from assessment netting should be trivial in relation to the overall adult mortality of a given population. In some cases, assessment fishing is limited for public relations reasons. Typically, the approach in such cases is to rely on live capture techniques with mark and recapture procedures to measure abundance and on restricted samples taken for autopsy. The level of exploitation generated by sampling should be determined.

Careful analysis of the components of variance (natural, process or background, and measurement or observational) will be required in nearly all cases because there are situations in which progressively increasing sampling intensity beyond some point yields little decrease in variance. There is a need for cost-effective sampling levels and strategies which minimize the sums of the squared deviations.

Sport fish harvests are moving quickly towards dominance, and the problems associated with assessing recreational catches precisely and coherently are enormous. The entire issue should be addressed urgently and this calls for improved and generalized methods for catch surveying. One critical need in effort evaluation is a means to assess the skill of anglers during creel survey interviews.

Even if a universal system of producing sport fishery catch data emerges, the effort data will remain difficult to use in fishery models without ancillary information about stock abundance. Assessment netting can provide these data and, more importantly, produce the spatially and trophically compre-

hensive measures of community health which are not readily obtainable through the species-selective fisheries.

New Information Needs

The central requirement for optimal fisheries management has always been for estimates of absolute stock abundance and biomass. Historically, these estimates were obtained on the basis of the economic importance of the fishery and/or the severity of the management problem. The need for generalized estimates has now become acute for several reasons including maximum stocking levels, multispecies management problems arising from but not confined to the rehabilitation era, the need for precision in quota setting related to the new allocation issues, and strategic planning for lakewide management of water quality and fisheries. These issues require an understanding of the dynamics of fish communities, which must be based on estimates of abundance or biomass for various species components, which, if not absolute, are at least realistically relative.

These new information needs are large and intractable and deal with broad ecological questions about fish community resilience, ecological efficiency in relation to community structure, and carrying capacity. These information needs are really not new, but are newly acute and demand new approaches.

Paloheimo and Regier (1982) emphasized the need for improvement in comparative capability to reduce or eliminate the need for long series analysis. This is a critical need because interpretation of the inevitable trends in fish community observation series requires controls against which stress impacts can be evaluated. Both time series and comparative measures of fish community health are thus necessary.

Management issues can be addressed in terms of the interactions of the biotic components of the ecosystems, and it will be necessary to do so. Equally, tests of new community models such as particle size spectrums (Borgmann 1987) make the needs for biomass measurements and for the measure of calibrating catches of organisms from different gears critical.

Both mark–recapture and catch–effort studies have produced acceptable population estimates of large adult fish. Small fish species and smaller members of larger species are difficult tc mark, tag, and handle in sufficiently large numbers to yield significant recaptures. Further, the abundance of smaller fish is difficult to estimate from catch–effort statistics because their natural mortality rates vary with predation levels.

A recent development which may help is the coded wire microtag (Monan 1985) which is injected into the nasal cartilage of salmonids. The tags are located magnetically at the time of recapture. Present technology allows for 120 000 lot identifications in the tag codes. In the future, mass marking of small nonsalmonid species may be feasible and detection with X-radiography or other approaches may permit live release.

The calibration focus can also be developed. Data are available about the selection properties of gill nets, but studies of efficiencies of various mesh sizes are rare (Hamley and Regier 1973). If this problem were solved, relative biomass spectra could be drawn for a large number of species down to the smallest sizes subject to capture in gill nets. There has also been work on mesh size effects on trawl catches (Ferguson and Regier 1963), but studies about areas swept and efficiency of capture for various fish species and sizes have not been extensive. Similarly, there has been extensive work involving the use of sonic tags to track the movements of fish, but very little has involved correlating fish behaviour with probability of capture in a fishing gear (Kushneriuk 1982). This aspect of calibration relates to relative capture of both different sizes and species and is obviously essential information for the construction of particle size spectra. Research in these areas should be given high priority.

Hydroacoustic approaches to fish counting have become very sophisticated in recent years and may prove especially useful for the enumeration of small fish. There are still problems with shallow-water and near-surface applications and with target shading in densely schooling fish. Nevertheless, target enumeration by depth strata and fish size has advanced significantly towards a rapid fish survey technique. While the search for improved technology and for "absolutes" in terms of fish biomass and numerical estimates continues, there is a tendency to delay reporting results until the ultimate improvements are achieved. Given that these may be years in emerging, it is important that current empirical relationships between target counts and fish catches are published.

The greater deficiency lies with the ability to "ground truth" the acoustic data. There has been little rigorous research into the catchability coefficients or selection properties of bottom trawls in the Great Lakes, and the understanding of the more recently adopted midwater trawls is at an even more primitive level. An alternative approach, using target counts from side-scan or regular echo sounders to "ground truth" the catches of different gears, for calibration purposes combines the two methodologies. Although this has not received much attention, it might be accommodated readily into the regular activities of assessment vessels.

This kind of calibration has a great deal of intrinsic attractiveness because it provides more direct insight into the variability in fish distribution. Nevertheless, even with a control with known sample variance, the number of replicates necessary to conduct a comparison between gears is high. This is true if the problem concerns comparing new fishing methods, replacing worn gear, or developing correction factors for comparison of data obtained by different assessment methods. These calibration needs cannot be optimally met through existing dedicated vessels because the power and deck equipment of the operational assessment vessels, as well as the gear characteristics, affect the sampling. Assessment programs should thus be designed with sufficient free vessel time outside the sampling routine to deal with the calibration needs.

There are, however, clear limits to the amount of flexibility which can be incorporated. There are exceptions, but normally deriving relative abundance and other vital statistics requires annual measurement. This means that ecologically important but unique or ephemeral events such as the explosion of the cormorant population in Lake Ontario (Christie et al. 1987), may not be easily added to programs based on fixed annual assessment budgets. Similarly, monitoring the status of physical habitat (wetlands, physical development, etc.) need not be carried out with annual frequency. In both kinds of work, the requirement is for strong cooperation between agencies with different mandates. Still, the continuity of observation will remain a most important consideration. Historical differences in approach, therefore, will often have to be linked by calibration, rather than compromised.

The generality that ongoing fish community observation series should be site specific raises questions about choice of site. In some cases, index sites for historical data series were

established on the basis of representativeness for a single species of economic importance. This may continue as an important criterion, but other niche descriptors such as depth, spatial area, and shoreline development should be considered. Sampling based on habitat stratification is essential to monitoring fish communities.

Generally, assessment which is sufficiently intensive to provide reliable estimates of relative stock abundance provides ample material for biological study. The cost for analysis of the samples (size, age, sex, state of maturity, stomach contents) may be many times the cost of collection of the specimens. This has always been a major constraint on the number of subsamples autopsied. As multispecies management requires information about community interactions, emphasis on the laboratory aspects clearly needs to be increased.

Similarly, invertebrates need to be monitored continuously and comprehensively. Integration of the fish and water quality concerns has extended to the analyses of contaminants in fish, but with only a few exceptions, integrated collection and analysis of biotic and physicochemical elements of the ecosystems has not occurred.

The problem of assessing the pelagic community may not be solved by simply improving midwater trawling technology. Pelagic salmonids are now sampled in angler surveys (especially in the recent popular fishing derbies) and during spawning. These samples are restricted in space and time and, more importantly, provide little representation of early life stages. For short-term salmonid management, this is not a problem. From the multispecies management perspective, however, the fish should be monitored continuously at all sizes as interactive components of the lake fish communities. This applies to both naturally and artificially supported stocks.

A similar problem exists with fish which occupy rocky bottoms of the Great Lakes, which are too rough for trawl sampling. These areas shelter large biomasses of small fish, which are important elements in food webs. Consequently, monitoring the status of these stocks has become increasingly important.

Policy Considerations

Four major principles emerge:

(1) The central requirement of assessment is continuity of observation through time.

(2) Assessment should be multifaceted to meet both short- and long-term needs of management. The latter in particular entails developing fish community monitoring and understanding.

(3) Assessment objectives should be made explicit, for priority setting purposes.

(4) Assessment techniques should be standardized to permit comparisons between jurisdictions.

Initiative Cost vs. Resource Value

The traditional approach to large fisheries has been assessment for stock conservation purposes. Observations led to regulatory changes, the results of which were evaluated by assessment. Ongoing monitoring and enforcement were regarded as the main components of management costs. Rules for defining the percentage of the value of a fishery which should be applied to assessment do not exist, but one could predict a priori high variability between nations and fisheries. It is, however, a truism that more funding for assessment is invested in large, valuable fisheries than in the smaller, less valuable ones.

The assessment–regulation–enforcement pattern was the only one of consequence in the Great Lakes until recently. The advent of successful salmonid planting and sea lamprey (*Petromyzon marinus*) control programs, however, broadened the assessment role to include the evaluation of these initiatives in an interactive way. One complication that this introduced was that while regulation adjustments had to be assessed over periods of years, the active management programs required short-term assessment to allow for midcourse adjustments. This has exposed some interesting contrasts in the separate approaches.

A related item is that priority setting for the allocation of assessment resources has been affected by a new accountability. Where regulation was and is the principal tool, program size was based on the importance of the fishery. During rehabilitation, program priorities were based on past or potential values of the collapsed fisheries in order to justify the public expenditures, including assessment. The magnitude of the real values of the fisheries is now being appreciated, but accountability continues to be tied to the levels of government spending. The focus is primarily on getting the best returns from hatchery fish and on effective lamprey treatment. Assessment of these programs at present takes precedence over the kind of stock assessment which would normally be tied to the value of the fishery.

By contrast, warmwater fisheries have never been managed by the intensive interventions applied to cold-water fisheries. Also, to the extent that self-sustaining cold-water fish communities are restored, accountability will return to the fishery values (sea lamprey control excluded). Currently, there is a great deal of concern among fishery managers about the ultimate mixture of fish which will emerge in the Great Lakes, either naturally or by way of human intervention. Recent advances in biolimnological understanding have demonstrated that the productive nearshore areas cannot be dissociated from the lake systems. Management initiatives and natural community dynamics will interact to greater or lesser degrees. It is clear that nearshore and offshore assessment should be integrated and of equal status. This means that the basic ongoing assessment programs should be tied to the perceptions, if not the realities, of what general resource values will be.

The need for evaluating the success of management initiatives against costs will remain important. In theory, these costs are associated with long-term benefits, diminish relative to the benefits with time, and should be amortized to hypothetical zero to more accurately represent public investment. The burden of rehabilitation costs, then, is not easily separable between the users of the fisheries resources. The tendency has been to assume that abuses of water quality led to losses of the fisheries resources, such that repair costs should be shouldered by the general public. The results of the fishery rehabilitation initiatives have shown that not to be entirely true. More importantly, the findings of Spencer and King (1984) and others suggest that mismanagement of the fisheries used by the smaller societal groups can affect costs of potable water for the broader society. These effects have not yet been fully quantified but suggest, at minimum, that assessment needs including the fishery elements should be placed in the broader context of societal aquatic resource use, rather than the narrower context of fish extraction

from the lakes. As Christie et al. (1987) pointed out, this broader approach to accounting will become increasingly necessary because as the control costs associated with the maintenance of steady-state fish communities will rise only slowly, the costs for general protection of the system will continue to rise sharply.

Ongoing Assessment Program

The broad, intractable management issues can only have approximate solutions at the present time. Exact solutions depend on finding answers to equally profound questions, relating to system resilience and ecological efficiency. Clearly, the best interest of management will be served by enhancing predictive capabilities. This requires research, which cannot be complete without the overview capabilities of assessment. The situation, therefore, requires shared data bases and close interactions.

The greatest obstacles to ongoing systematic asssessment lie with the urgent issues which emerge with unpredictable frequency. These are matters requiring immediate attention and often field investigation. The key issue is how to retain sufficient response capability while protecting the ongoing assessment program.

Another feature of rehabilitation is that improved fisheries have brought new allocation disputes. The tendency has been to invest in initiative-cost assessment, which is often only marginally related to the broader questions at issue. In some cases, the relative shares taken by the disputants can be determined by independently operated and funded surveys. Where the questions concern the size of the resource to be shared, they can only be answered by resource-value assessment.

When the initiative-cost elements and the exigent issues have been segregated from the assessment program requirements in priority and budget setting, the remaining issues concern the ongoing program elements and the calibration and (related) standards of measurement. These are often complex technical issues, but can be relatively quickly overcome. The central issues involve the move from a single- to multispecies (community) approach and the necessary additional flexibility for assessment programs.

Human Resources

The progression from localized research-oriented fishery studies, which depended on assessment data, to the large-scale institutionalized assessment programs was an inevitable consequence of the dramatic regrowth of the Great Lakes fisheries. This has been a healthy development because it makes possible rigorously systematic long-range assessment programs. Nevertheless, it calls for integrated programs.

Scientists will work well together at the holistic level, if a common cause can be found. The opportunity for novel scientific work at the ecosystem level and in an arena so vitally important to human society cannot fail to provide this rallying point. Scientists whose careers have been dedicated to individual reductionist studies should be welcomed in the holistic science framework because the only integration problem will be to show relevance to the larger objectives. Participation problems often arise because scientists fear contributing their talents to a team and not having their individual creativity recognized. This is a difficult and essentially unresolved problem which deserves to be given high priority in the development of any team undertaking. Given common causes and sufficient opportunity to discuss resolution of this issue, satisfactory solutions can be developed.

Operating Resources

In stressing the statistical and biological uncertainties, especially as related to the small fishery assessment problems, we do not wish to convey pessimism, nor to suggest that the work cannot be accomplished without massive new infusions of funding. Rather, a great deal can be accomplished at contemporary budget levels by focussing assessment objectives and setting priorities accordingly. A central requisite, however, is a well-informed administration. Realizing that at best there will be a progressive consolidation of the soft biological answers to hard-edged management questions, managers should develop an understanding of the need to provide program flexibility for biologists to practice science.

Savings are possible through the more effective use of human resources. The history of aquatic research on the Great Lakes is unmatched in its scope, intensity, and excellence. Because of the programs and public dedication to improved water quality for fisheries, the ranks of scientists representing many disciplines in government service have increased the reservoir of human resources. To integrate these resources into generalized plans for the development of fish community assessment and research will require increasing communication among agencies, governments, and academia. Funding opportunities are now emerging to encourage this process. Various State Sea Grant agencies in the United States now provide considerable support to universities for aquatic research. In Canada, the Ontario Renewable Resources Research Grant Fund is similarly providing financial support to Ontario universities. The challenge is to have these agencies provide the fora within which discussion about common cause can occur.

Not least among the positive aspects of the funding question is the new involvement of fisheries interests with broader environmental concerns. The objectives and programs of the International Joint Commission have featured fish and fisheries with increasing prominence over the past decade. The most recent development has been work towards the establishment of remedial action plans for the many areas of concern which have been identified around the lakes by the International Joint Commission. These plans will all contain fish community components, and equally important, there will be clear needs to integrate these studies with routine lake assessment. A similar and somewhat more advanced event on the Canadian side recently saw federal funding provided for fisheries assessment via the Canada–Ontario Agreement on Water Quality. These are positive developments and signal recognition of the trend to integration. They especially emphasize the importance of settling the fisheries assessment policies and priorities soon to provide for clear integration of the new funding.

Conclusion

The shift in viewpoint this paper calls for is basic. In the confusion of crisis management, the tendency has been to accept assessment as established technology. We suggest now that we must use science to develop the tools needed by ongoing Great Lakes fishery management and skillful coordination to optimize the rate of development while at the same time properly attending to the exigent needs.

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Meeting Future Information Needs for Great Lakes Fisheries Management[1,2,3]

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Description of information needs for management of Great Lakes fisheries is complicated by recent changes in biology and management of the Great Lakes, development of new analytical methodologies, and a transition in management from a traditional unispecies approach to a multispecies/community approach. A number of general problems with the collection and management of data and information for fisheries management need to be addressed (i.e. spatial resolution, reliability, computerization and accessibility of data, design of sampling programs, standardization and coordination among agencies, and the need for periodic review of procedures). Problems with existing data collection programs include size selectivity and temporal trends in the efficiency of fishing gear, inadequate creel survey programs, bias in

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age estimation, lack of detailed sea lamprey (*Petromyzon marinus*) wounding data, and data requirements for analytical techniques that are underutilized by managers of Great Lakes fisheries. The transition to multispecies and community approaches to fisheries management will require policy decisions by the management agencies, adequate funding, and a commitment to develop programs for collection of appropriate data on a long-term basis.

La description des besoins en information pour la gestion des pêches des Grands Lacs est compliquée par les modifications récentes dans la biologie et la gestion des Grands Lacs, l'élaboration de nouvelles méthodes d'analyse et une évolution du mode de gestion qui abandonne l'approche traditionnelle monospécifique pour une approche plurispécifique ou axée sur les communautés. Il faut régler un certain nombre de problèmes généraux portant sur la collecte et la gestion des données et sur l'information nécessaire à la gestion des pêches (résolution spatiale, fiabilité, informatisation et accessibilité des données, conception des programmes d'échantillonnage, normalisation et coordination parmi les organismes, et nécessité d'une révision périodique des méthodes). Les programmes actuels de collecte des données connaissent certains problèmes: sélectivité par taille et tendances temporelles dans l'efficacité des engins de pêche, insuffisance des enquêtes sur la pêche sportive, distorsion dans l'estimation de l'âge, absence de données détaillées sur les blessures causées par la lamproie marine (*Petromyzon marinus*), et besoins en données pour les techniques d'analyse qui sont sous-utilisées par les gestionnaires des pêches dans les Grands Lacs. L'adoption d'approches plurispécifiques et axées sur les communautés exigera que les organismes de gestion prennent certaines décisions, disposent d'un financement satisfaisant et s'engagent à élaborer des programmes visant la collecte à long terme des données nécessaires.

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This paper is based on discussions of the working group on data requirements and assessment methodology that took place during and subsequent to the International Symposium for Assessment of Stocks and Prediction of Yields (ASPY). The purpose of this paper is to document the information needs of Great Lakes Fisheries managers, including (1) raw data (e.g. lengths of individual fish), (2) information necessary for interpretation of raw data (e.g. information about size selectivity of fishing gear), (3) descriptions of how data were collected and recorded, (4) data collected routinely from fishermen, (5) data collected by management agencies during assessment activities, (6) data already in existence, and (7) data that should be collected in the future. The determination of information needs necessitated discussions about analytical techniques because analytical methodologies for assessment and the kinds of data collected are related in a fundamental way.

This paper is not a cookbook of detailed solutions to specific problems. The number and complexity of the issues discussed precluded the formulation of detailed solutions. Instead, a number of important issues raised by the working group are discussed and some general solutions proposed.

Background

The Great Lakes of North America are vast heterogeneous ecosystems that have undergone dramatic changes due to overexploitation, introductions of exotic species, and pollution and the subsequent rehabilitation programs including sea lamprey (*Petromyzon marinus*) control, phosphorus control, and the resurgence of native stocks and massive stockings of exotic salmonids. These factors have left the Great Lakes in a state of flux (Loftus and Regier 1972; Berst and Spangler 1973; Christie 1973; Hartman 1973; Lawrie and Rahrer 1973; Wells and McLain 1973), leading Steedman and Regier (1987) to suggest that Great Lakes ecosystems will not reach equilibrium states for many years and that the nature of the equilibrium states that might become established is not known.

Consequently, Great Lakes fisheries management is also in a state of transition. There is an emerging perception among fishery managers that current theory and methodologies, based on single-species approaches, are inadequate for understanding and managing Great Lakes fisheries resources (Steedman and Regier 1987). A reasonable hypothesis is that a multispecies and/or community approach is needed to manage Great Lakes fisheries. We defined a multispecies approach as one that obtains information about groups of interacting fish species and manages the individual species in the context of their interactions. A community (ecosystem) approach was defined as one that obtains information about a wider variety of species (e.g. vertebrates, invertebrates, and plankton) and environmental factors (e.g. weather, water temperatures, and contaminants). The multispecies/community approach, then, requires integration and synthesis of information from a variety of sources in such a way as to permit managers to predict the effects of management actions on species assemblages or communities.

More than three decades ago, Hile (1954) suggested that successful management of Great Lakes fisheries would have to involve consideration of interactions between species. Numerous authors (Cohen and Stone 1987; Loftus et al. 1987; O'Gorman et al. 1987b; Schlesinger and Regier 1983; Skud 1982; Taylor et al. 1987) have demonstrated well the important consequences of species interactions and environmental effects on the dynamics of exploited fish stocks. The mechanisms responsible for changes to Great Lakes fish stocks may be due to interactions among species, the environment, or to a combination of biological and environmental factors. It is not clear, therefore, what sort of models and data would lead to better understanding and management. The movement towards multispecies/community management is a most important issue, therefore, in the context of fisheries assessment and information management because additional and new kinds of data will be required to support the multispecies/community approach.

Other factors contribute to the current state of flux in Great Lakes fishery management. Foremost among these is the

increasing importance of recreational fisheries (often directed primarily at introduced species) and declining importance of traditional commercial fisheries for native species. This situation has led to a need for reliable information about recreational harvests. The diverse nature of the fisheries also complicates management of Great Lakes fisheries. Both the recreational and commercial fisheries typically include small boats that fish relatively small amounts of gear near home ports and large, well-equipped boats that can fish large amounts of gear at potentially any location in the Great Lakes. Catches by small boats cannot be ignored because in the aggregate, their harvest and effect on local stocks may be substantial. Comparison of effort and catch-per-unit-effort data is complicated, therefore, by difference in the effectiveness of fishing effort.

Additional uncertainty about the information required for management arises because analytical methodologies that are often used for management of marine fisheries (cohort and catch-at-age analysis) are seldom used in the Great Lakes, as the requisite data (e.g. age structure of the catch) are not generally available. Another factor contributing to this uncertainty has been movement away from local assessment of fisheries for purely scientific purposes to institutionalized large-scale collection of data for management. It has become increasingly important that the data collected from Great Lakes fisheries serve the purposes of both science and management.

The challenges, then, with respect to data and information for management of Great Lakes fisheries during this transition period are to (1) develop and improve procedures for collecting, maintaining, and disseminating data and information, (2) ensure that both short- and long-term needs for information are met, (3) collect information that will allow improvements to the management and understanding of Great Lakes fish stocks, and (4) facilitate the transition to multispecies/community management. These challenges are also emphasized in Christie et al. (1987).

General Issues

Spatial and Temporal Resolution of Raw Data

Information is lost when data are aggregated according to large geographic areas. Raw data for relatively small geographic areas can be aggregated, but information about small areas cannot be obtained if the raw data were aggregated originally by large areas.

The collapse of the herring fishery in the Wisconsin waters of Lake Superior during 1936–78 illustrates the consequences of overaggregating data. Total catch and catch-per-unit-effort for the Wisconsin waters of Lake Superior did not reflect changes in the abundance of lake herring (*Coregonus artedii*) until just before the entire fishery collapsed. Selgeby (1982) reexamined the original commercial fishing reports and determined that the fishery had sequentially overexploited six localized stocks. The existence of the six herring stocks and their overexploitation may have been evident to managers, if the commercial catch and fishing effort data had not been summarized for large geographical areas, but had been reported on the basis of a finer spatial scale. Beverton et al. (1984) and Winters and Wheeler (1985) documented similar problems in connection with marine fisheries.

A useful system for specifying locations based on 5′ and 10′ grids of latitude and longitude has been used increasingly in the collection and recording of data from Great Lakes fisheries. This system can be recommended because it provides sufficiently fine spatial resolution and flexibility for reaggregation during analysis.

Reliability of Data

Reliability of data is influenced by the design of sampling programs, accuracy and precision of measurement, and the reliability of the system used to manage (record, store, maintain, and retrieve) the information. Recent covert operations, in connection with the enforcement of commercial fishing regulations in the Great Lakes, suggest that commercial catch and fishing effort data may not be reliable because of unreported catch by fishermen (Hartman and Ross 1985). Lake whitefish (*Coregonus clupeaformis*) fisheries in much of Lake Superior are regulated on the basis of lake trout (*Salvelinus namaycush*) caught incidentally; the lake whitefish fisheries are closed when the quota for lake trout has been reached. This system of regulation, therefore, encourages underreporting of the lake trout catch. Assignment to individual fishermen of quotas for two or more statistical districts can lead to inaccuracies in commercial catch and fishing effort data because fishermen who exceed their quota in one district can surreptitiously apply catch from one district to another and thereby corrupt the information from both areas. These examples illustrate problems in the measurement of commercial catches and fishing effort, but reliability of measurement also applies to recreational catch and effort data. In cases where bias and imprecision in measurement cannot be eliminated, an attempt should be made to estimate the magnitude and direction of the problem.

Contrast and Information Content of Data

When possible, management activities should contrast and maximize the information content of data. The "adaptive management" approach (Milliman et al. 1987) seeks to increase the information content of data by manipulating variables that control the quantity or characteristic of interest. The effects of lake trout stocking on the abundance of lake trout can, for example, be determined from stocking and catch-per-unit-effort data (Lawrie and MacCallum 1980). Managers might elect to manipulate stocking levels over a wide range to gain further insights into the effects of stocking on abundance, insights that would not be realized if stocking levels were held constant. This approach does not necessarily involve risk to the resource. Walters et al. (1986), for example, used a simulation model to show that the contribution of natural reproduction to recruitment of lake trout might be determined without long-term effects on lake trout rehabilitation, if stocking programs were interrupted for 1 yr.

Computerization

Management and analysis of large volumes of data require computerization to realize a satisfactory return on the resources invested in data collection. Some data currently being collected are not being preserved in computerized form, and large volumes of historical Great Lakes fisheries data have never been computerized or analyzed. Many of these existing data sets have been underutilized principally because of the difficulties involved in accessing and analyzing data that are not stored in a computer-retrievable form. Existing information should be computerized to make it more accessible and formats should be standardized to permit comparisons between jurisdictions.

Rapid computerization and improved accessibility would

enable managers to monitor fisheries, particularly those regulated by quota systems, in "real time" (i.e. on a nearly instantaneous basis). Delays in the collection, compilation, and analyses of commercial and sport fishing data leave managers uncertain as to how much of an allotted quota has been taken by a specific fishery at any given time. Many current systems for collection and management of commercial fishing data require several months for information about catch to become accessible to managers. In contrast, dockside data collection and rapid computerization have substantially reduced the time required for transfer of information to managers of Lake Erie fisheries (J. Paine, Ontario Ministry of National Resources, Wheatley, Ont., pers. comm.). A creel survey system implemented on Lake Ontario provides estimates of total monthly harvest by boat anglers within 10 d after the end of each month (Lester and Trippel 1985). It will become more important to obtain real time information about harvest as quotas are used increasingly to control harvests of Great Lake fishes.

Time Series Information

Many kinds of data, e.g. catch and fishing effort data, are most useful to managers in long, uninterrupted time series and are necessary for detection of long-term trends in the condition of a fishery or fish community as well as better application of many techniques for stock analysis (i.e. surplus production models, delay-difference models, cohort analysis, and catch-at-age analysis) and to enhance predictive capabilities.

Managers should maintain the continuity and comparability of data in existing time series because interruptions in a series of data can reduce substantially the value of the information. A single missing observation can be a serious obstacle in the application of some analytical methodologies. Managers should consider the effects of regulation changes that may impact data that are routinely collected and compiled in long time series.

A commitment to the continuity of important time series should be a matter of policy in agencies that manage Great Lakes fisheries. In a climate of limited resources, there is a tendency for agencies to concentrate on collection of the information required for resolution of critical, short-term problems, at the expense of information required for long-term management and evaluation.

Designs for Sampling

The design of sampling programs is an issue that has received insufficient attention. Populations should be sampled in a statistically sound manner to minimize bias and variance of estimates and to permit detection of changes in populations or communities. Managers should determine the level of precision required in parameter estimation. The next step should be the design of a satisfactory sampling program, including definition of strata, determination of times and locations for sampling, and specification of required sample sizes. Estimators should be selected early in the process of designing the sampling program and evaluated for efficiency, robustness, and applicability. The problems involved in sampling large, poorly defined populations of fish, at a reasonable cost, are not trivial and it would be appropriate often to seek the help of a fisheries statistician. The costs and effort involved in careful design of sampling programs will be defrayed, in many cases, by reduced costs of sampling, improved reliability of the data collected, and increased precision of estimates.

The issue of designs for sampling programs will require more explicit and systematic attention as additional information needs are recognized and new sampling programs are implemented during the transition to multispecies and community assessment and management. For example, sampling locations for assessment netting are sometimes chosen to maximize the information obtained about a single species. It may be better to stratify sampling programs by habitat in order to obtain information about entire communities.

Matters of Policy

Better coordination and integration within and among agencies would increase comparability of information, improve efficiency in collection, and lead to better management. Progress is being made towards the coordinated, lakewide assessment and management of some Great Lakes fisheries resources, as evidenced by the recent adoption of lake trout management plans by the various lake committees.

Agencies should also commit to periodic reviews and evaluation of policies, strategies, and approaches to the collection and management of data. Periodic review is particularly necessary as systems for information management are developed and as the information needs of management and condition of Great Lakes ecosystems change.

Data Availability and Publication Rights

Management of Great Lakes fisheries would benefit from broad accessibility to data from a variety of disciplines. Agencies and individuals involved in data collection programs have, however, a substantial investment in the information collected. Furthermore, well-intentioned researchers, who are not familiar with a particular data set, may be misled by special characteristics of the information. Broad accessibility to data should not be regarded as automatic permission to publish the results of analysis. The release of data for publication should be contingent on written permission from the agency or individual responsible for the data and on an opportunity for that agency or individual to participate in the research and publication.

Issues Related to Information Needs for Unispecies and/or Traditional Approaches

Temporal Trends in Efficiency of Fishing Gear

There is little information about changes over time in the efficiency of fishing gear used in commercial and recreational fisheries on the Great Lakes, although such information is necessary for improved resolution of trends in catch and fishing effort data, as well as for the use of many analytical techniques. Changes in the efficiency of gear used in the Great Lakes have occurred in large steps, with major changes in the design or materials used in the construction of fishing gear and gradually, with incremental changes in gear design, fishing techniques and skill of the fishermen. There have been attempts to develop correction factors for these major changes in efficiency (Pycha 1962; Selgeby 1982; Collins 1979; Collins 1987a, 1987b), but incremental changes, which may over time amount to substantial increases in efficiency, have been largely ignored. The effects of changes in the efficiency of fishing gear have been confounded, in some cases, by dramatic changes in the density of target stocks (Pycha 1962; Cucin and Regier 1966). A further complication has been the lag (in some cases more than a decade) between the time improved gear is employed and the time at which information about the change in efficiency is

reported. Detailed information about the construction of fishing gear should be obtained whenever possible.

Temporal trends in the efficiency of recreational fishing gear have been largely ignored, despite substantial improvements to angling gear. Trolling gear used by anglers to harvest lake trout has, for example, become much more efficient, as the wire lines and sash weights have been replaced by nylon fishing lines with downriggers and as temperature guages, chemicals, speedometers, echo sounders, radios, and devices for radio-assisted navigation have become popular. Information about the type of gear used by anglers and changes in the efficiency of that gear will become crucial as recreational fisheries expand.

Efficiency of Different Types of Fishing Gear

Information about relative efficiency of different types of fishing gear used in the Great Lakes is generally lacking. Correction factors for relative efficiency could be used to combine information for different gears. This would be particularly advantageous when the dominant gear in a fishery (e.g. commercial gill nets) is replaced by another sort of gear (trap nets or angling gear) and it is necessary to compare data collected at different times. When controlled experiments cannot be conducted to determine the relative efficiency of a new fishing gear, the two types of gear should be used simultaneously for several years, so that relative efficiencies can be estimated.

An alternative to obtaining information about the relative efficiency of fishing gear is to obtain an estimate of "effective fishing effort" by dividing the product of the estimates of total catch and total effort by the catch-per-unit-effort of a standard year (Ricker 1975). This estimate of "standard effort" can be used when it is not possible to calibrate gear efficiencies (e.g. sport fisheries). Further, this estimate has the advantage that any reliable measure of relative abundance (e.g. hydroacoustic data) can be used instead of traditional catch-per-unit-effort information.

Size Selectivity of Fishing Gear

Lack of information about the size selectivity of common types of fishing gear is an ongoing problem in interpretation of data from Great Lakes fisheries. Many analytical techniques used by managers (e.g. determination of mortality rates from catch curves) require either that the probability of capture in the fishing gear be equal for fish over a range of size classes or that the catch of different size classes be adjusted to account for differences in capture probability (Ricker 1975). The gear used to sample fish in the Great Lakes is size selective, but correction factors for fish of different size have not, in general, been developed. The development of correction factors for size selectivity is not a simple problem, but techniques are available (McCombie and Fry 1960; Berst 1961; Regier and Robson 1966; Hamley and Regier 1973; Hamley 1975; Rudstam et al. 1984; Jensen 1986; G. R. Spangler and J. J. Collins, unpubl. data). Approximate correction factors for trawls can be developed from information about the length and girth of fish and size of the gear (Pauly 1984).

Information about Recreational Fishing and Harvest

Creel surveys in much of the Great Lakes are totally lacking, of insufficient scope, or statistically unreliable despite the fact that recreational fishing has become increasingly widespread. Recreational fisheries have expanded in size to such an extent that their biological, economic, and political impacts surpass those of the commercial fisheries throughout most of the Great Lakes. Well-designed creel surveys are, for this reason, required for sound management. The problems involved in designing and implementing creel surveys for large areas are not inconsequential. Charter boat fisheries and fishing derbies for salmon and lake trout are, for example, characteristics of the recreational fisheries that will require special and coordinated approaches for assessment. The problems involved in obtaining biological information (e.g. age, sex, and growth data) as well as catch and fishing effort data from creel surveys need to be addressed.

Tagging and Marking

Lake trout reared in hatcheries and released into the Great Lakes have traditionally been marked by clipped fins. A problem with this approach is that the number of distinct, usable combinations of fin clips is limited. Consequently, fin clips used lakewide for an entire age class of stocked lake trout are repeated at relatively short intervals (5 yr) so that there may be two or more age classes of lake trout with identical fin clips present in the lake. Age-specific survival is not estimated for Great Lakes salmonids, despite extensive and ongoing mark and recapture programs. Brownie et al. (1985) stated "we cannot emphasize too strongly that, based on our current knowledge, there is no valid way to estimate age-specific survival rates from only bandings of the young. There are, however, a number of mark and recapture models that can be used to estimate age-specific survival if several cohorts of adults are marked and recaptured, in addition to the juveniles."

Coded wire tags (Jefferts et al. 1963; Parker 1967; Monan 1985) are a new technology that offer the potential for marking and identification of thousands of different groups of stocked lake trout (Elrod and Schneider 1986). Coded wire tags can be used to evaluate a variety of factors that might influence the performance of stocked fish (e.g. genetic strain, rearing method, season of release) and will improve the quantity and reliability of information obtained about fish stocked in the Great Lakes. Interjurisdictional cooperation, however, is again a requisite for realization of the full benefit of this new technology. Lack of cooperation will undoubtedly lead to delays in the exchange of information about tag recoveries between jurisdictions and the loss of information.

Ageing

Another issue related to information for management of Great Lakes fisheries is the possibility that age data obtained by identification of annual marks on scales is badly biased. There is now abundant evidence that scales underestimate the true age of slow-growing fish in northern latitudes (Beamish and Harvey 1969; Aass 1972; Sikstrom 1983). An analysis of ageing techniques has shown, for example, that lake trout older than age 7 or 8 tend to be underaged by the scale method (J. M. Casselman, unpubl. data). Furthermore, the magnitude of the bias increases with the actual age of the lake trout. It is likely that the use of scales has resulted in errors in the ageing of alewife (*Alosa pseudoharengus*) from the Great Lakes (O'Gorman et al. 1987a). Managers should validate (Beamish and McFarlane 1983) techniques currently used to age fish taken from the Great Lakes. If current techniques are found wanting, then corrective measures (i.e. use of otoliths or other bony structure for ageing

and correction for bias in existing data) will be necessary. This issue requires immediate attention because age information is the vital component of many key parameters considered in the management of a fishery.

Sea Lamprey

Systematic programs for collection of adequate quantities of detailed lamprey wounding data are needed. Information about sea lamprey wounding is important because sea lamprey predation can have significant effects on the populations of valuable prey species, such as lake trout and lake whitefish, in the Great Lakes (Pycha 1980; Spangler and Collins 1980; Spangler et al. 1980). Levels of lamprey wounding (measured as mean lamprey wounds per fish, or proportion of fish with at least one lamprey wound) were, until recently, the only known, observable link between lamprey and the mortality they inflict. Unfortunately, most of the available data are not sufficiently detailed to allow meaningful analysis. Eshenroder and Koonce (1984) recommended standardization in collection and reporting of lamprey wounding information, and Jacobson (1986) discussed the design of sampling programs for sea lamprey wounding data. A recent study in Lake Ontario indicates that it may be feasible to directly estimate lamprey-induced mortality by recovering lamprey-killed lake trout in quantitative bottom trawls (R. Bergstedt, U.S. Fish and Wildlife Service, Oswego, NY, pers comm.).

Analytical Techniques

Some analytical techniques, widely used for management of marine fisheries (e.g. catch-at-age analysis and cohort analysis), have not been applied extensively in the Great Lakes because necessary data, particularly about the age and size composition of the catch, are not abundant. Managers should determine the potential benefits and utility of these techniques and decide whether or not to collect the requisite information. Sampling recreational and commercial landings for age and size data will require carefully designed programs.

Issues Related to Information Needs for Multispecies and Community Approaches

Multispecies and community approaches to assessment and management of fisheries are more complex and require more extensive information than traditional unispecies approaches. To make progress towards the goal of multispecies and community management, it will be necessary to develop coordinated programs that are funded adequately for extended periods. The requirement for long-term program support makes it necessary for agencies to commit to the multispecies/community approach at the policy level, realizing the relative infancy of the multispecies/community approach. Periodic review of developing approaches will be necessary to improve programs.

Existing data should not, however, be neglected, as compilation, coordination, computerization, and careful analysis of existing data will contribute much to the understanding of multispecies and community issues in the management of Great Lakes fisheries. This point is particularly important in connection with "natural experiments" that are not likely ever to be repeated (e.g. interactions between lake trout and lamprey before lamprey control and the alewife die-offs in Lake Michigan).

The major question with multispecies and/or community approaches to assessment and management of Great Lakes fisheries is not whether, but rather, when and how. It is difficult, however, to specify the information requirements for a multispecies or community approach because of the lack of well-developed multispecies models and assessment methodologies. Multispecies models exist (Pauly 1979; May et al. 1979; Mercer 1982; Skud 1982; Pikitch 1987; Daan 1987; J. Beyer, unpubl. data), but their applicability to the Great Lakes is uncertain. In this connection, Christie and Loftus (unpubl. data) warned of a "Catch-22" situation in which data for multispecies/community assessment are not collected because of a lack of models and models are not developed for lack of data. It is clear that greater understanding of interspecific and community interactions is needed for better management of Great Lakes fisheries. There is, however, considerable uncertainty about what should be measured and the level of temporal and spatial scale required to effectively document community interactions. Uncertainty as to the best approach should not prevent scientists and managers from assembling data that are potentially useful for understanding and managing Great Lakes ecosystems in a multispecies/community context.

Transition to a Multispecies/Community Approach

Information requirements during the transition to a multispecies or community approach to management will depend, to a large extent, on the nature of the evolving models and analytical techiques selected by managers. There are a variety of approaches to multispecies and community assessment which vary in sophistication, data requirements, and assumptions. As no single model is applicable in all unispecies situations, it is unlikely that a single multispecies model will come to dominate the field of multispecies and community assessment. It seems clear that multispecies and community assessment should be approached by a variety of avenues. Policy-makers must recognize the necessity for a diversity of approaches.

The costs and materials required will likely be an obstacle in transition to multispecies/community assessment. Careful planning, cooperation, implementation, and evaluation of new sampling programs will reduce costs. The use of information from unispecies assessments and initial application of new sampling programs to restricted areas of the Great Lakes will also reduce costs. Implementation of hydroacoustic methods for assessment, and other technologies for obtaining data at low cost, will further reduce the costs of collecting data useful for traditional and multispecies/community objectives.

It may be better, instead of diverting existing personnel and boats, to allot funds for additional ships and personnel to undertake multispecies and community assessments. The additional ship and personnel time could be allocated flexibly as opportunities and proposals for new sampling programs develop. The speed at which multispecies and community assessment programs develop would be increased with minimized impact on existing assessment programs.

Bioenergetics models are bridging the gap between the traditional unispecies and multispecies/community approaches to assessment and management. These models have been used to address questions concerning the dynamics of single species

(Kerr 1971; Stewart et al. 1983; Eck and Wells 1983), but show greatest promise in connection with the multispecies, particularly predator–prey dynamics (Stewart et al. 1981; Eck and Brown 1985; Eck and Wells 1987; Kitchell and Hewett 1987). Bioenergetics models require detailed information about behavior, physiological processes, mortality, and abundance. Although much of the necessary information can be obtained from laboratory studies, some information from field studies is usually necessary. Bioenergetics models are an excellent example of the application of a developing technology to the problems of multispecies and community assessment.

In the remainder of this section, two possible approaches to the transition towards multispecies/community assessment and management are described.

Measure Everything

In the absence of certainty about what kinds of information to collect, it may be best to collect as much information as possible about the organisms and environmental factors in a particular community. Analysis of such data would, presumably, reveal the types of data that were most useful. The "measure everything" approach, although expensive on a large scale, could be applied to small areas of the Great Lakes or an inland lake for the purpose of determining the importance of different types of information. This strategy merits consideration because if data are collected only where there is a proven need for the information, then progress towards identification of relevant data and development of multispecies/community models will be impeded.

Piggyback Approach

The "piggyback" approach assumes that multispecies and community models for fisheries management will require information (e.g. catch, fishing effort, growth, abundance, diet, etc.) that can be derived from traditional unispecies assessment. A collection of unispecies assessments would be the basis for the transition to a multispecies/community approach. Any sort of biological or environmental information that was thought to be important could be collected on a trial basis. In some cases, new information could be obtained with little additional effort (e.g. stomach content data could be obtained during standard assessment netting). New sampling programs, however, would have to be developed, as with the sampling of benthos or invertebrates. After an initial period of data collection and analysis, the relevance of the information could be assessed. Information that appeared to be relevant would become a permanent part of routine assessment. Data that did not appear to be relevant would not be collected during future assessments. Information from assessment of forage species and species of lesser economic value, as well as information about environmental factors, invertebrates, plankton, phytoplankton, and special interactions among species, would be collected gradually and, at least initially, on an experimental basis.

An advantage of this approach is that it is adaptive and flexible. Decisions about the kinds of information to be collected would be guided by the data requirements for existing or newly developed models, economic constraints, and the knowledge of biologists familiar with the ecosystems under consideration. Collection and evaluation of new types of information could be restricted to one or more small sections of the Great Lakes to reduce expense during evaluation. A disadvantage of the piggyback approach is that the transition to a truly multispecies or community approach to management would be delayed.

Conclusion

There are a number of general problems in the collection and treatment of information for management of Great Lakes fisheries (i.e. spatial resolution, reliability, computerization and accessibility of data, design of sampling programs, standardization and coordination among agencies, and the need for periodic review of procedures). Problems in connection with traditional approaches to management and assessment are the need to correct for size selectivity and temporal trends in the efficiency of fishing gear, inadequacies in existing creel survey programs, bias in techniques for ageing fish, lack of comprehensive and detailed sea lamprey wounding data, and data requirements for analytical techniques that are probably underutilized. Existing data have been underutilized in many cases. Also, as suggested by Christie et al. (1987), better coordination of human and material resources and improved integration of water quality information and fisheries assessment data can achieve much without necessarily great increases in funding.

Managers, understanding the desirability of multispecies and community approaches to fisheries management, should develop policies and programs that will result in collection of the requisite data. The transition to a multispecies/community approach will require commitment by agencies at the policy level because of the uncertainty and potential expense involved. Periodic review of approaches to multispecies assessment will be required as information and experience accumulate, Great Lakes ecosystems are rehabilitated, and management goals change.

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Concepts and Methods of Community Ecology Applied to Freshwater Fisheries Management[1]

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In this paper we review selected theory, hypotheses, and methods of community ecology with reference to fisheries management. Community ecology is concerned with theoretical and empirical studies of the behavior of species assemblages over space and time. Ideas that have evolved from these types of studies concerning hierarchical organization, resource partitioning, food webs, structural integration, stability, complexity, and production and their relevance to fisheries management are discussed. One main conclusion confirmed by the ASPY Symposium is that the productivity of fish communities is determined by energy inputs, nutrients, edaphic factors, and habitat variables but that the distribution of the production by species is strongly influenced by interactions between species. A related conclusion is that species interactions are size dependent because of morphological, physiological, and behavioral constraints on predator–prey relationships, resulting in a hierarchical organization. Further, density-dependent interactions (predation, competition) within and between species influence growth rates, size distributions, and age-specific mortality and reproductive rates, and vice versa. Anthropogenic factors such as fishing, nutrient enrichment, introduction of exotic species, and chemical contaminants tend to act differentially at the level of species, but due to interdependencies between species their effects are propagated at the community level by disrupting its size- and niche-structured organization. Fish communities can be managed as relatively discrete functional units, but dependency on whole system dynamics ultimately necessitates an ecosystem perspective. Development of a more quantitative theory of fish community dynamics will require improved descriptions of species interactions (food web structure, ontogenetic histories, resource partitioning, and body size dependency), better characterization of complexity, stability, and successional change in fish communities, additional knowledge of energy transfer through aquatic ecosystems, and improved methods of estimating biomass distributions in fish communities. Comparative studies over space and time and experimental and adaptive management are appropriate ways for fishery scientists and managers to acquire this knowledge.

Les auteurs examinent une théorie, des hypothèses et des méthodes choisies pour l'étude de l'écologie des communautés dans le contexte de la gestion des pêches. L'écologie des communautés se rapporte à des études théoriques et empiriques du comportement de groupements d'espèces dans l'espace et le temps. Les auteurs développent les idées qui se dégagent de ce genre d'étude concernant, d'une part, l'organisation hiérarchique, le compartimentage des ressources, les réseaux alimentaires, l'intégration structurale, la stabilité, la complexité et la production et, d'autre part, leur pertinence pour la gestion des pêches. Une des principales conclusions étayées par les études présentées au Colloque ASPY veut que la productivité des communautés piscicoles soit déterminée par les apports énergétiques, les bioéléments, des facteurs édaphiques et des variables environnementales mais que des interactions entre les espèces influent fortement sur la distribution de la production par espèce. Une autre conclusion veut que les interactions spécifiques dépendent de la taille à cause de restrictions morphologiques, physiologiques et

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comportementales sur les relations prédateur–proie, qui donnent lieu à une organisation hiérarchique. De plus, les interactions interspécifiques et intraspécifiques liées à la densité (prédation, compétition) influent sur les taux de croissance, les distributions des tailles et les taux de reproduction et de mortalité liés à l'âge, et vice versa. Des facteurs anthropogènes comme la pêche, l'apport de bioéléments et l'introduction d'espèces exotiques et de contaminants chimiques ont tendance à agir par action différentielle au niveau spécifique mais, à cause d'interdépendance entre les espèces, leurs incidences sont disséminées au niveau de la communauté dont elles désorganisent la structure selon la taille et la niche. Les communautés piscicoles peuvent être gérées en tant qu'unités fonctionnelles relativement isolées mais en raison de la dépendance vis-à-vis de la dynamique d'un système global il faut en fin de compte considérer l'écosystème tout entier. La mise au point d'une théorie plus quantitative de la dynamique des communautés de poissons nécessitera des descriptions améliorées des interactions spécifiques (structure du réseau alimentaire, cycle ontogénétique, compartimentage des ressources et dépendance vis-à-vis la taille corporelle), une meilleure caractérisation de la complexité, de la stabilité et de la succession chez les communautés piscicoles, d'autres connaissances sur le transfert énergétique dans les écosystèmes aquatiques et des méthodes améliorées pour l'estimation des distributions de la biomasse dans les communautés piscicoles. Des études comparatives dans l'espace et le temps ainsi qu'une gestion expérimentale et souple sont des moyens permettant aux scientifiques et aux gestionnaires des pêches d'acquérir ces connaissances.

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Fisheries ecologists possess a wealth of information about fish species life histories, their niche characteristics, and the factors that affect fish reproductive success and recruitment to fisheries. Fish species compositions and relative abundances can often be predicted for particular habitat types, say shallow–warm versus deep–cold lakes. Success has been limited, however, in predicting fishery yields and in anticipating changes in species abundances associated with particular environmental perturbations. Fisheries ecology and particularly community ecology is concerned with improving the ability to predict the dynamics of fish populations and with developing a theoretical framework which will lead to a quantitative approach to managing and rehabilitating fisheries resources.

We argue that a need exists for improved understanding of community and ecosystem dynamics in fisheries management. This argument is based, in part, on the failure of traditional single-species models to effectively predict fish yields (e.g. May et al. 1979; Mercer 1982; Sissenwine 1984), but more importantly is founded on the accumulating empirical evidence of the governing role of species interactions (predation, competition) in the production dynamics of aquatic ecosystems (Christie 1974; Svardson 1976; Skud 1982; Ursin 1982a; Gislason and Helgason 1985). Comparative and trend-through-time studies documenting the responses of fish populations and communities to anthropogenic factors such as fishing, eutrophication, and species introductions (e.g. Loftus and Regier 1972) have been especially useful in the development of conceptual models concerning the assembly, regulation, and transformation of fish communities (Regier and Cowell 1972; Kerr 1977; Ryder and Kerr 1978). These concepts are now increasingly being incorporated into management programs for freshwater and ocean fisheries (Loftus et al. 1978; Ontario Ministry of Natural Resources (OMNR) 1978a, 1984; Laevastu et al. 1982; Tyler et al. 1982; Ursin 1982a; Ryder and Edwards 1985).

In practice, fisheries managers need to understand the underlying processes that regulate fish communities (Regier and Henderson 1973). While their problem continues to be the determination of sustainable yield from a standing stock (Larkin 1977; MacLean and Evans 1981), it is now recognized that variation in abundance of fishes in a population depends on parental stock size and structure, interspecific interactions, and abiotic environmental factors (Sissenwine 1984). Until relatively recently, process-oriented studies have been aimed primarily at the effects of stock size and environmental variability on fish populations, with little attention to interspecific effects. Fisheries managers now require models which include the effects of competitive and predatory interactions between species on the structure and production dynamics of the fish communities they wish to manage.

Our aim in this paper is to provide an overview of the application of community-based approaches to freshwater fisheries management. We review the concepts, theories, and supporting empirical studies of fish community ecology in an attempt to develop a synthesis of present knowledge. Further, we review the methodologies and applications presently available for study and management of freshwater fish communities and focus attention on three basic questions related to the application of community theory to management: (1) What constitutes a fish community? (2) What are the key functional relationships underlying community structure? (3) What constitutes a manageable set of structural components or processes that could be used to model community responses? The first question seeks to define what it is that we wish to manage, the second to identify how the community functions, and the third to describe an adequate quantitative model for the purpose of managing it.

The paper is divided into three main parts. The first deals with structural and functional properties of fish communities. Here we provide a working definition of community and briefly discuss the concepts of hierarchical organization, resource partitioning and competition, structural integration, and stability and complexity. The second part surveys the various methods of fish community analysis, including trend-through-time approaches, comparative studies, multivariate classification, food web models, particle size theory, and field manipulation experiments. The third part provides a synthesis of the previous two sections and returns to our original questions concerning structure, function, and development of a quantitative model of community ecology. In that section, we discuss the choice of

ecological scale and management perspective, the implications of niche and body size relationships in the assessment of the effects of exogenous factors (nutrients, fishing, introductions) on fish community dynamics, management applications of community dynamics information, and research needs.

Structure and Function of Fish Communities

The term community has been applied in the ecological literature to describe plant and animal assemblages varying in complexity from taxonomic groups of a few species (e.g. fishes or littoral zone fishes) to entire ecosystems of plants and animals (e.g. Odum's (1971) biotic community). One major problem is to define the temporal and spatial boundaries of the community to be managed or studied. The most important criterion is that the bounds encompass the structural and dynamic properties of the system. In practice this usually requires some reduction of the total complexity by identifying species components and scales deemed appropriate for the specific management or study goals.

Fish communities have been defined as assemblages of interacting species (Kerr and Ryder 1977). Ryder and Kerr (1978) used the adjectives harmonic to describe highly integrated fish communities and astatic for loose assemblages. They argued that harmonic communities are stable and more persistent than the astatic ones that usually result from human intervention. Their definition incorporates structural and functional properties of communities, harmonic referring to the self-regulated complementarity of species abundances, resulting from interaction among compatible, coevolved forms.

For our purposes, we begin by defining community as an assemblage of species residing in whole or in part in a particular area or habitat. This is strictly a structural definition without functional implications. Fish production, however, is dependent on edaphic factors, allocthonous inputs, physical habitat, and energy (Ryder et al. 1974; Ryder 1982; Schlesinger and Regier 1982), as well as the way in which these components are partitioned among species in the aquatic ecosystem. The structure and production of a fish community will depend, therefore, on the production of other trophic components (Oglesby 1977; Matuszek 1978; Borgmann 1982, 1983, 1987; Hanson and Leggett 1982; Mills and Schiavone 1982; McQueen et al. 1986; Minns et al. 1987), the mix of co-existing fish species (Daan 1987; Evans and Waring 1987), and habitat constraints imposed by the abiotic environment (Ryder and Kerr 1978; Marshall and Ryan 1987). Since fish represent only one taxonomic component in the hierarchy of aquatic production systems, a logical question is whether fish communities are sufficiently discrete ecologically to be perceived as functionally coordinated subunits. In other words, can they be managed independently of the whole system when they are clearly dependent on it? Our synthesis suggests that fish communities do have functional properties amenable to management control. These properties, including discreteness and homeostatic mechanisms (self-regulation), and the supporting evidence for their existence are discussed in later sections of the paper.

Hierarchical Organization

A primary organizational feature of aquatic ecosystems is their hierarchical structure which, in part, is captured by the familiar concept of levels of organization. For example, ecosystems are composed of communities, populations, and individual organisms representing a stepwise progression in complexity. Each level of the hierarchy is composed of the elements of the next lower level. The dynamics at each level, however, are influenced by biotic and abiotic factors interacting within and between levels. In contrast, the hierarchical concept described by O'Neill et al. (1986) focuses on the process rates of functionally discrete biotic and abiotic components of complex systems.

O'Neill et al. (1986) suggested that the level-of-organization concept of ecological hierarchy, while representing one useful way of conceptualizing aquatic ecosystems, is too restrictive as a universal way of subdividing ecosystems into their functional components. They argued for a more flexible and precise approach which emphasizes a "function-preserving fractionation" that identifies structural discreteness and associated differences in process rates. Hierarchical structures can be either nested (e.g. leaves, trees, and forests) or nonnested . An example of the latter in aquatic ecosystems is found in their particle size distribution. Body size progresses from small to large particles and from rapid to slow rate processes, respectively. Rates of metabolism, growth, reproduction.and natural mortality all decline as body size increases, while longevity, in contrast, increases. These allometric relationships are fundamental to the hierarchical size structures of these systems (Sheldon et al. 1977).

The central premise of hierarchy theory is that organization in complex systems results from differences in process rates (Allen and Starr 1982). The hierarchical approach recognizes the functional redundancy inherent in the taxonomic diversity of ecological systems, which in effect enables the complexity to be decomposed into its fundamental organizational structure. For example, in aquatic ecosystems, different species often have similar functions (guilds) and single species can perform different functions under different circumstances or during different stages of ontogeny. O'Neill et al. (1986) argued convincingly that hierarchical theory, by focusing on process rates, provides an operational method through which the functional structure of the ecosystem can be extracted from empirical data, rather than from arbitrary designation of taxonomic or other components, such as levels of organization or trophic levels.

One concensus achieved at the ASPY Symposium is that body size is of primary importance, both in transfer of energy in aquatic ecosystems (e.g. Borgmann 1987; Dickie et al. 1987) and, ultimately, in determining predator–prey relationships and demographic characteristics within fish assemblages (e.g. Daan 1987; see also Gislason and Helgason 1985). Prey capture is restricted by mouth gape in many aquatic organisms, leading to subtle but pervasive effects on community structure. Several contributors to the ASPY Symposium and others have discussed the effects of body size on physiological and demographic variables and the implications for community structure (Fig. 1):

(1) Metabolic costs (units of oxygen consumed per individual per unit time) increase with body size, but the rate of increase per unit mass declines (Peters 1983). Growth efficiency (K_1) declines with body size for specific size classes of prey (the upper and lower boundaries of the shaded envelope bounds the range of prey sizes consumed) partly because more energy is expended per unit of energy captured as predator size increases and prey size stays the same (Fig. 1A) (Borgmann 1987; Evans and Loftus 1987; see also Kerr 1971; Kerr and Ryder 1977).

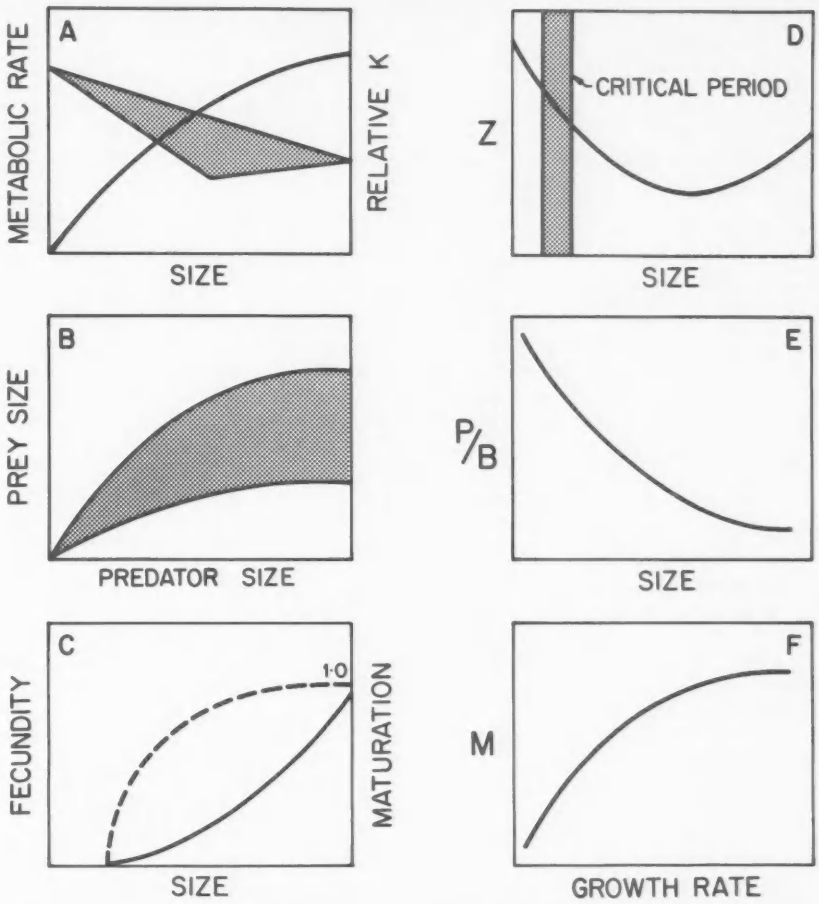

FIG. 1. Functional relationships of fishes that are dependent on body size. (A) Relative growth efficiency is indicated as a shaded envelope and metabolic rate is in terms of oxygen consumed per individual per unit time; (B) the size range of prey consumed increases but reaches a plateau as predator size increases; (C) the proportion mature is shown as a broken line; (D, E, and F) the ordinates are Z (total instantaneous mortality), P/B (production/biomass ratio), and M (instantaneous natural mortality rate).

(2) The prey size that is consumed increases directly with predator size (Fig. 1B) and the range of prey sizes eaten usually increases (e.g. Zaret 1980; Evans and Loftus 1987). The strategy that maximizes growth efficiency (optimal foraging theory) is to take the largest prey available with the least cost. Transferring from the lower limb of the growth efficiency envelope (Fig. 1A) is contingent on a predator's ability to shift from the smallest available prey size to the largest during ontogeny (Keast 1983). Ontogenetic shift from one prey type to another provides a key example of how size-linked processes can influence community structure (Crowder et al. 1987). Any factor that affects the availability of prey, through intra- or interspecific mechanisms, will also change energy flow and community structure (Mills and Schiavone 1982). For example, loss or reduction of a top predator will lower the predation mortality of its prey, causing an increase in their density and a concomitant increase in intraspecific competition, thereby reducing their growth efficiency and mean size (Persson 1986; Colby et al. 1987). Stunting of perch populations is an example of this type (e.g. Persson 1983; Rolf 1986).

(3) Fecundity and percent of a population that is mature increases with body size (Fig. 1C). Reproductive output reaches a maximum within a certain size range because mortality rapidly reduces the number of adult fish. These life history parameters, therefore, are growth and size dependent (Rolf 1986).

(4) Total mortality (Z) is a function of size (Fig. 1D). At small size, fish have high vulnerabity to predation, which extends the concept of a starvation-linked critical period for pelagic larva (May 1974) to a community context linking intra- and interspecific factors to mortality through size-dependent processes (Peterson and Wroblewski 1984). Beyond a certain size, Z will increase with size (age) through senescence (Craig and Kipling 1983; Gislason and Helgason 1985; Laevastu and Bax 1986).

(5) Production to biomass ratio declines with body size (Fig. 1E) (Sheldon et al. 1977; Banse and Mosher 1980; Borgmann 1982; Dickie et al. 1987) due in part to decreasing growth

efficiency (Fig. 1A) (Borgmann and Ralph 1985). The actual trajectory of the curve will depend on the level of nutrition and growth efficiency (Fig. 1A) (Kerr and Ryder 1977) of the specific population involved.

(6) Natural mortality (M) increases with growth rate (Fig. 1F) (Beverton and Holt 1959; Adams 1980; Pauly 1980). Slower growth rates in stunted stocks result in smaller size at maturity and lower fecundity, but are offset by a lower rate of natural mortality. This reciprocity explains how net reproduction (Rolf 1986) can remain constant under these circumstances.

These relationships (Fig. 1) illustrate the key mechanisms underlying some of the dynamic, size-linked processes which govern fish community structure. Changes in growth rates and body size are thus directly linked to demographic variables, and these can be readily transformed by interspecific factors. These relationships are also the avenues via which various perturbing forces (exploitation, nutrient additions, chemical contaminants, heated effluents, invading species) can affect life history parameters of individual species, thereby causing transformation of entire communities (e.g. Hurley et al. 1986).

Structural Integration of Fish Communities

Several authors at the ASPY Symposium argued that fish communities are structurally integrated and, therefore, confined within certain bounds by internal mechanisms which control both structure and production (Christie and Loftus, 1987b; see also Ryder and Kerr 1978; Ryder et al. 1981). These authors and others suggested that coevolution (Roughgarden 1983a, 1983b) confers certain structural conservatisms on mature assemblages so that variability is less and resilience and resistance to disturbance are greater than in less mature or randomly generated assemblages (Pimm and Hyman 1987). If fish communities are more than random assemblages of interacting species, they should demonstrate characteristics of stability (i.e. resistance, resilience, persistence) not possessed by random assemblages. The question of self-regulation or homeostasis of fish communities has important implications for fisheries management. For example, resistance to change implies that some degree of stress can be tolerated without causing transformation of the whole system (Kerr 1977).

What evidence exists to support the hypothesis of homeostasis in fish communities? A useful synthesis in this regard was the SCOL Symposium (Loftus and Regier 1972), which focused on the effects of ecological stresses (exploitation, eutrophication, and introductions) on salmonid-dominated communities in oligotrophic lakes. Of the many insights gained from the SCOL Symposium, three stand out with reference to community homeostasis: first, oligotrophic lakes of the north-temperate zone had historically similar indigenous fish assemblages, suggesting the strong influence of habitat, but also possibly a consistent pattern of community succession; second, these fish communities have some capacity to persist under moderate exploitation pressure; and third, similar patterns of fish community transformation occurred under extreme perturbation (i.e. loss of top piscivores, major shifts in abundances of prey species, and establishment of large stocks of exotic species, often small planktivores). These observations suggest structural conservatism among these species assemblages, resistence to change, and the integrative influence of large piscivores on community structure.

Fish communities described in the proceedings of the SCOL Symposium, therefore, appear to consist of similar species groups rather than random collections of populations with little or no integration. If these assemblages of populations are highly integrated and persistent, it is important to understand how the integration is achieved in order to extend the general findings of the SCOL papers.

Recurrence of discrete assemblages of species is a primary requisite of the coevolved-community hypothesis, but discreteness can possibly be explained simply in terms of environmental requirements of species (i.e. habitat). The key to this issue is to determine which factors govern species richness, composition, and abundance and, importantly, to be able to separate the habitat and community effects. Numerous structural and functional properties of communities pertaining to this question were discussed at the ASPY Symposium and by others in the recent literature:

(1) Species richness is a function of lake area (Evans and Loftus 1987) or watershed area (Mahone 1984), but species composition is also a function of habitat characteristics. Thermal regime, for example, can be a primary determinant of community type (Marshall and Ryan 1987). Barbour and Brown (1974) identified the linkage between species richness and habitat diversity in their study of North American and African lakes. These papers indicate that species structure is shaped by space and habitat characteristics, implying certain limited configurations for species interactions and coexistence. The ideas presented are consistent with concepts of niche complementarity and species packing (Werner 1977), but do not explain the underlying, demographic constraints (Werner and Gilliam 1984) which actually set the bounds on species composition. Both habitat and community factors appear to be important.

(2) Loss of a top predator causes major changes in community structure (Evans and Waring 1987; Pimm and Hyman 1987). Changes in lake trout (*Salvelinus namaycush*) density in Lake Simcoe were followed by changes in abundances of several prey species. Christie et al. (1987a) reported similar changes in Lake Ontario linked to loss of lake trout and introduction of exotic Pacific salmon.

(3) One species can affect the abundance of other species directly by predation (Christie et al. 1987a; Colby et al. 1987; Daan 1987; Kitchell and Hewett 1987; see also Hackney 1979; Nielson 1980; Zaret 1980; Hixon and Brostoff 1983; Loftus and Hulsman 1986; Walters et al. 1986) or indirectly by utilizing food or spatial resources (competition) used by other species (Brown et al. 1987; Colby et al. 1987; Crowder et al. 1987; Eck and Wells 1987; see also Fraser 1972, 1978; Johnson 1977; Werner and Hall 1977; Hanson and Leggett 1985, 1986; Jude and Tesar 1985; Persson 1986).

(4) Fish communities are hierachically structured by body size, frequency of occurrence of particles being inversely related to body size (Borgmann 1987; Minns et al. 1987; Sprules and Munawar 1986; see also Kerr 1974a, 1974b). Energy transfer and storage is facilitated by size-linked metabolic and predator–prey relationships (Dickie et al. 1987), but ultimately, production is dependent on nutrient level (Hall et al. 1970; Minns et al. 1987).

(5) Invasion by exotic species disrupts community structure, usually resulting in shifts in species abundances and, in some cases, extinction (Evans and Loftus 1987; see also Zaret and Paine 1973). Species invasion might be facilitated by prior destabilization of a fish community (Evans and Waring 1987; Pimm and Hyman 1987; see also Christie et al. 1972; Loftus 1976).

(6) Stability of a community appears to be a function of complexity (Pimm and Hyman 1987), more mature (possibly more integrated) communities being less prone to invasion. This suggests a successional trajectory of community development which through random invasion and species interaction leads to organization among species populations.

(7) Habitat is a primary determinant of species composition (Marshall and Ryan 1987; see also Adams and Olver 1977; Johnson et al. 1977; Harvey 1978; Tonn and Magnuson 1982; Tonn et al. 1983; Eadie and Keast 1984). Habitat change, species interactions, and climatic perturbations can interact to influence dominance shifts between interacting, indigenous species such as lake whitefish (*Coregonus clupeaformis*) and yellow perch (*Perca flavescens*) (Evans and Waring 1987; see also Numann 1972; Svardson 1976; Svardson and Molin 1981) and other species pairs (Skud 1982).

(8) Coexistence between species appears to be achieved through complementarity of form and behavior (Keast and Webb 1966; Ali et al. 1977; MacLean and Magnuson 1977; Ryder and Kerr 1978; Gatz 1979).

(9) Similarity in habitat use and (or) trophic status often coupled with some environmental change can result in displacement of one species by another (Colby et al. 1987; Evans and Loftus 1987). Examples include northern pike (*Esox lucius*) and muskellunge (*E. masquinongy*) (MacCrimmon and Skobe 1970; Harrison and Hadley 1978; Inskip and Magnuson 1983), alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) (Evans and Loftus 1987), centrarchid species (Werner 1977), and brook silversides (*Labidesthes sicculus*) and inland silversides (*Menidia beryllina*) (McComas and Drenner 1982). Marine examples are also known: rockfish species (Larson 1980) and gobiid species (Edlund and Magnhagen 1981). These observations are consistent with morphological differentiation between coexisting fish species in freshwater, form being a reflection of function and species niche (Keast and Webb 1966; Gatz 1979; Mahone 1984).

(10) Ontogenetic niche shifts can be dramatically affected by population parameters (growth rates, survival rate, age of maturity), and as a consequence, interaction between species is also affected (Crowder et al. 1987; see also Werner and Gilliam 1984). Intra- and interspecific competition can influence growth rate (e.g. Persson 1986) and the duration spent at each ontogenetic stage. Growth efficiency is size dependent (Borgmann 1987; Dickie et al. 1987; Evans and Loftus 1987); therefore, factors affecting growth rates of early life stages could have a major bearing on population dynamics and community structure.

(11) Food or food availability appears to be limited in most fish communities, in view of rapid growth and (or) survival compensations observed when intra- or interspecific density changes occur (Colby et al. 1987; Evans and Waring 1987; see also Svardson 1976; Johnson 1977; Hanson et al. 1983; Perrson 1986). This suggests that fish communities are very tightly structured through resource sharing.

(12) Prey switching by piscivores, the best examples of which involve introduced prey (Christie et al. 1987a; Evans and Loftus 1987; see also Martin 1970), appears not only to increase fitness of the predator by minimizing time spent foraging or maximizing net energy yield (Schoener 1971) but also tends to regulate prey densities and to result in community stability (Erlinge et al. 1984).

To summarize, fish community structure in temperate freshwater lakes is dependent on habitat characteristics modified by intra- and interspecific interactions, while total (community) fish production appears to be primarily determined by energy, edaphic, and nutrient effects. Predation has a dominant role in the organization of communities as does resource sharing among species within and between guilds (functional species groups). The concept of limiting similarity appears to apply to fish communities, as indicated by the diversity of form and function of fishes in indigenous assemblages, the susceptibility of very similar forms to dominance shifts, and nonrandom distribution of morphological traits (Gatz 1979). Present knowledge of fish community dynamics is not inconsistent, therefore, with the notions of coevolution and competition proposed by some to explain their structure. An alternative hypothesis that fish communities are structured by resource sharing (competition) and predation among species with similar environmental requirements, without implying coevolution, is equally well supported by the available evidence, although it seems unlikely that predator morphologies and life histories have evolved independently of their primary prey (Ali et al. 1977; MacLean and Magnuson 1977).

TABLE 1. Evidence of resource partitioning in freshwater fish communities.

Resource	References
1. Temperature	Henderson and Fry 1987; Brandt et al. 1980
2. Depth	Crowder 1984; Koelz 1927; Moyle 1973
3. Light	Ryder 1977; Ryder and Kerr 1978
4. Oxygen	Matthews and Hill 1980
5. Turbulence and velocity	Finger 1982
6. Vegetation	Laughlin and Werner 1980
7. Substrate	George and Hadley 1979
8. Time	Kelso 1978; Floyd et al. 1984; Schlosser and Toth 1984
9. Feeding	Keast and Webb 1966; Mittelbach 1984; Werner and Hall 1979; Moyle 1973
10. Reproduction	Balon 1975; Orth 1980

Resource Partitioning and Competition

Evidence for partitioning of a wide range of resources by freshwater fishes is abundant and clear (Table 1) (Schoener 1974; Ross 1986); the processes that bring it about, however, and the reasons for the extent of partitioning are controversial (Schoener 1982, 1983, 1985; Connell 1983; Roughgarden 1983b; Strong et al. 1984). The main weakness of descriptive evidence of resource partitioning is that it leads persuasively to the conclusion, by circular reasoning, that competition has brought about the effect (Sale 1979). Another failing of most descriptive studies of partitioning is that the abundance of the resource is not known; the historical trends in the availability of the resource may help to explain the presence or absence of competition (Hurlbert 1978). For example, Schoener (1982) hypothesized that competition would be most intense when resources are leanest. At best, descriptive studies of partitioning will only assist in the formulation of hypotheses. The role of interspecific interaction in determining the structure of fish communities will probably be clearer if experimental manipulations of competitors and resources are performed by removals and introductions. Descriptive studies, however, allow one to focus such experiments.

In Schoener's (1983) review of field experiments on interspecific competition, most published reports (90%) showed that competition was prevalent. However, of the 148 studies, only 4 of the 22 competition experiments in freshwater were concerned principally with fish (Werner and Hall 1976, 1977, 1979; Fausch and White 1981). In contrast, Connell (1983) concluded that when the effects of intra- and interspecific competition were separated, the proportion of studies in which interspecific competition was evident was much reduced. Furthermore, Connell (1983) suggested that even then, the incidence of competition was exaggerated because positive results were more likely to be published. In this symposium, resource partitioning was inferred by several authors to be a function of interspecific competition (Colby et al. 1987; Crowder et al. 1987; Eck and Wells 1987; Evans and Loftus 1987; Evans and Waring 1987; Henderson and Fry 1987), but none provided direct experimental evidence of the type reported by Fraser (1972, 1978), Werner (1977), and Hanson and Leggett (1985, 1986) showing that competition was actually occurring.

Pianka (1976) stated that competition occurs when resource availability is limited and one organism or population interferes with or inhibits another. This appears to be common in fish communities where intra- and interspecific density-dependent changes in growth and survival rates have frequently been observed (e.g. Johnson 1977), although it is often difficult to separate the effects of competition from those of predation. The question of the role of interspecific competition in resource partitioning (Schoener 1982, 1983; Connell 1983) would appear to be central to understanding how fish communities are organized. If the niche is a singularly important concept for understanding competition and the structure of fish communities, it is evident that more research should be directed towards studies of habitat requirements, species interaction, and resource partitioning.

Stability and Complexity of Fish Communities

Fish community complexity can be characterized by species richness (number of species), connectance (proportion of all possible interactions), evenness (the equitability of species abundances), and diversity (various measures that combine evenness and species richness) (Pimm 1984). The relationship between these structural properties of communities and their inherent stability (propensity to return to equilibrium following perturbation; Pimm 1984) has generated much interest among ecologists and is of importance to fisheries managers trying to sustain optimal yields. The notion of population equilibrium is central to the concept of stability. Dynamic equilibrium occurs, in the case of randomly fluctuating fish populations, when "there are finite average populations around which the animal numbers fluctuate with steady variances" (May 1973). Characterization of population levels and their variances provides a basis for understanding the influences of both internal (e.g. species interactions) and external (e.g. fishing) factors affecting the dynamics of fish communities (Ursin 1982b). Remarkably, long-term abundance trends and variances have been recorded and analysed for relatively few fish populations. Lacking empirical data, fisheries managers have proceeded on the premise that fish populations are or should be relatively invariant and that any major change from the imagined equilibrium level is a signal of system transformation. Demonstration of equilibrium requires spatially or temporally replicated data and quantitative description of the inherent trends and deviations to identify the existence, shapes, and sizes of the stability domains for various fishery systems. The "landscape of these attractor domains" (Peterman et al. 1979), which includes the factors that affect the fitness of species, is equally important to understand. The above definition of stability, which we employ, is not inconsistent with the concept of stability domains discussed by Peterman et al. (1979), which suggests that several equilibrium states (domains of attraction) may exist for a single system.

Pimm (1984) defined a set of characteristics, including resilience (how quickly a system returns to equilibrium), persistence (the time a variable persists before being changed to a new value), resistance (the degree to which a variable changes following a perturbation), and variability (the variance or comparable measure of population densities over time), which can be used to statistically describe the stabililty of a community. Holling (1985) noted that these definitions emphasize the steady-state condition as opposed to the dynamics of discontinuous behavior which, he concluded, is an inherent property of ecological systems. Holling (1985), in contrast with Pimm (1984), defined resilience as "the ability of a system to maintain its structure and patterns of behavior in the face of disturbance" and emphasized the importance of events far from equilibrium near the boundaries of a stability domain.

The value of these criteria of community stability for assessing the status of fish communities was addressed in detail by Pimm and Hyman (1987). They pointed out that stability can mean many things but that the concept of community stability can be effectively investigated only if it is divided into its more tractable components. They framed their discussion within the context of community succession and suggested that invasion may become progressively more difficult as succession progresses. A corollary to this is that perturbed communities, which might have been relatively mature at the time of the imposition of stress, should become more susceptible to invasion (Christie et al. 1972; Loftus 1976). This theory of ecosystem development states that succession follows a predictable trajectory: as communities mature, they become more tightly organized and efficient in terms of energy transfer and storage (Odum 1981). Pimm and Hyman (1987) provided a conceptual approach by which these ideas could be tested using commercial fisheries data.

Community complexity can be described using simple descriptors, such as richness, which give equal weight to all species, or compound ones which combine richness and relative abundance of species into a single index. The primary purpose of these indices is to provide a means of describing the state of a community over space and time (Patil and Taille 1979). There is little uniformity in the way in which diversity and evenness indices of community complexity have been calculated in the scientific literature, although several authors have addressed the question of standardization (Hill 1973; Peet 1974; May 1975; Routledge 1979, 1980, 1983; Taille 1979; Alatalo 1981; Washington 1984).

One of the most commonly used diversity indices is the Shannon–Wiener index H' (e.g. Marshall and Ryan 1987; R. A. Ryder and S. R. Kerr, unpubl. data), the so-called information theoretic of the Shannon and Weaver (1949) mathematical theory of communication (Johnson 1970). H' has also been used extensively in studies of competitive resource use but, we caution, has been criticized on this account (Hurlbert 1971, 1978; Hill 1973; Peet 1974).

Information theory defines information as a displacement

from randomness or as the negative of the amount of entropy. The concept of entropy has considerable appeal within the context of community ecology because it provides a holistic descriptor of the degree of organization (or alternatively disorder) of complex aggregations of species. Smetanin et al. (1984) applied information theory to describe temporal changes in two developing fish communities and found different patterns of change in complexity and entropy, but did not speculate on the causes or on community stability. This approach to describing complexity and organization would appear to have as yet untapped potential as a research and management tool.

Pimm and Hyman (1987) discussed the concepts of community complexity and stability in the context of multispecies fisheries. They raised questions concerning the connection between successional state (complexity, organization) and stability characteristics (persistence, resistance, resilience, and variability) of perturbed and unperturbed fish communities. In order to address these questions, descriptions of community complexity and organization are required. A prominant postulate of fisheries ecology is that unperturbed communities are more stable than perturbed ones, yet no quantitative analyses exist to convincingly document this. Description of community complexity, coupled with statistical descriptions of stability, would provide a means of doing so. Analyses of this type would also help to provide a more quantitative view of succession, the mechanisms of invasion and the effects of perturbations caused by fishing or nutrients, for example. Odum (1985) outlined a suite of expected ecosystem responses under stress that link species diversity and successional state with changes in species size, productivity, and life history variables, many of which are already observed by fisheries managers.

Another aspect of deciding whether a community is stable or not concerns the space and time scales selected for study. It also depends on the particular view adopted, an interest in the relative abundance of organisms, or rather, in whether species are simply able to persist, i.e. presence or absence (Connell and Sousa 1983). These authors discussed the evidence needed to evaluate ecological stability and showed the difficulty of establishing the existence of equilibria. They support the Eltonian view that variation in the numbers of one species directly and indirectly affects the numbers of other species, and that the variation is often irregular in period and amplitude. Connell and Sousa (1983) concluded that an appropriate approach to the question of stability is to determine whether species persist rather than to require the existence of stable equilibria. This focuses attention on the limits within which a system can persist and on the mechanics through which population abundance is regulated. From a management perspective, however, a more practical solution would be to select appropriate spatial and temporal scales and to determine how to enhance the natural regulatory mechanisms that either keep the system where it is or cause it to shift to a more desirable stability domain. Accordingly, Peterman et al. (1979) argued that resource managers need to know not only the limits for existence, but also the domains of attraction and their boundaries to effectively manage ecological systems. A key consideration in any management abstraction is recognition of the implications of the spatial and temporal scale dependency embedded in the model.

Methods and Models for Fish Community Analysis

ASPY contributors reported on temporal (trend-through-time studies), spatial (comparative studies within and between lakes), structural (community complexity, food webs, particle size distributions), and functional (predation, resource partitioning) variation in fish communities and addressed questions of stability, habitat requirements, predator–prey relationships, and intra- and interspecific competition as factors affecting species abundances, productivity, and fishery yields. In this section we discuss the approaches and methods employed and the main findings.

Trend-Through-Time Approach

Predictions of the future abundances of populations in a community, and projections of how proposed interventions may affect these abundances, are required by managers of fishery resources. A common assumption in the prediction of future abundances is that the observed history of abundances of the stock will be repeated; i.e. the resource is either in steady state or cyclic. Time series analysis will suffice to predict the future of stocks where this assumption is valid and where the magnitude of proposed interventions would be insufficient to disrupt the historic regulatory mechanisms. Additional information will be required, however, for astatic or perturbed communities were there is no expectation that the past history will be repeated or in instances where proposed interventions are expected to swamp or disrupt the historic regulatory mechanisms. This is the information that knowledge of community dynamics can provide.

Single-species analyses used in fisheries stock assessment and yield prediction are often more complex than time series analyses but have underlying assumptions in common: either the resource is in a steady state (basic yield per recruit analysis) or historic patterns will repeat themselves (stock and recruitment relationships). When are these assumptions tenable? Walters (1987) analysed the relationships between stock size and net production for six northeast Atlantic herring (*Clupea harengus harengus*) stocks. In only three of these stocks was a sufficient time series of data available to determine if the history of the stock would indeed repeat itself. In two of these three stocks, the available evidence suggests that the relationship between stock size and net production was different when the stock increased, compared with when it decreased. There was no evidence to indicate whether this "pattern" was a characteristic of the stock or its environment, and no evidence to indicate whether this pattern was repeatable. In only one of the six stocks was sufficient information (32 yr) available to determine that the relationship between stock size and net production had remained consistent over the time that the stock had been studied. Methodological information on survey efficiency and catchability can also be critically important to the analysis of population time series, as was seen for the 47-yr creel survey on Lake Opeongo (Shuter et al. 1987).

Walters (1987) suggested that statistical descriptions of the variation in abundance of a stock may be of more use in management than agonizing over the causation of variation that cannot be controlled. Of course, the end result of relying on the historic statistical description is that an optimum management approach focuses on the short term because, in this instance, the assumption that the recent past history of the stock will repeat itself is reasonably well supported by observational data. Long-term management scenarios are ineffective, in part, because the statistical description may be insufficient, and also because the influence of other species is unknown. Thus, Walters concluded that when harvest rates are fully controllable, then the "optimum policy is 'myopic' and involves

pretending either that (1) the current environmental state will persist indefinitely, (2) when a trend is evident, then the next environmental state in this trend will persist indefinitely, or (3) when the persistence (P_S) of environmental states is low, then future states will occur at random."

What role, then, does information of community dynamics have in the analysis and modelling of trend-through-time fisheries data? One role is as a modifier of the assumptions of single-species analyses, notably the assumption of a constant rate of natural mortality over different size and age classes of fish. This assumption of a constant rate of natural mortality over the life of a fish is "inherently improbable" (Hislop 1984), but there have, until recently, been a lack of verifiable replacement mortality schedules. Daan (1987) presented results from the multispecies extension of virtual population analysis (VPA) where, instead of assuming a constant rate of natural mortality for the various age classes of a stock, the major part of natural mortality is estimated from the predation by other species/age groups in the analysis. Natural mortality among young fish was estimated to be much higher than previously assumed in single-species VPA. Although the impact of this adjusted mortality schedule on short-term catch projections appeared to be insignificant, the impact on longer-term management objectives would be considerable. Indeed, Gislason and Helgason (1985), in a similar study, concluded that "a higher natural mortality for the younger age groups will change both the yield per recruit and the mesh size assessments. It thus seems likely that much of the current advice, which is based on calculations where the same natural mortality has been applied to all ages, is wrong."

Community dynamics information has a role in the extension of stock and recruitment analysis from correlative statistical analyses (the fitting of stock and recruitment data to a set of generic curves) to the proposal and testing of specific functional relationships. Skud (1982) indicated the need to include community interactions in the analysis of stock size over time and noted that apparent correlations of environmental variables with stock size may not be maintained over time as the community composition changes. B. E. Skud (unpubl. data) proposed an extension of the Ricker stock and recruitment model to account for juvenile buffering of predation on recruits.

Another application of community dynamics information in the analysis and modelling of trend-through-time data is to extend the optimum policy in management from a single-species to a multispecies management approach. Multispecies management advice has, in the past, varied from the deductive reasoning of Gulland (1982) to the complex ecosystem models of Anderson and Ursin (1977) and Laevastu and Larkins (1981), but such advice has yet to be generally accepted. The first step in gaining acceptance of the role of community dynamics in analysis of trend-through-time data is to demonstrate its usefulness in describing historic and current data. Multispecies VPA (Daan 1987) and holistic ecosystem simulation (Laevastu and Larkins 1981) have produced different and (hopefully) more accurate interpretations of historic data. Viewed in another way, we might ask: what can be learned about community dynamics through the analysis of trend-through-time fisheries data? Cohen and Stone (1987) described the use of multivariate time series analysis to indicate species interactions in the Canadian fisheries of Lake Superior. Similarly, Evans and Waring (1987) applied time series and correlation analyses to test for intra- and interspecific interactions for five species in Lake Simcoe, Ontario. Pimm and Hyman (1987) discussed the concepts of community stability and succession and also described how time series data can be analysed to search for changes in community dynamics.

Fisheries ecology is rich in comparative and time series data (e.g. SCOL, Loftus and Regier 1972; PERCIS, Colby 1977; ASPY). While these approaches clearly have limitations (Strong et al. 1984), due to undocumented environmental effects, ecological catastrophes, observational error, and absence of clear hypotheses, it is apparent that important inferences about community structure and dynamics can be obtained by analyses of these types of data (e.g. Christie et al. 1987a; Cohen and Stone 1987; Evans and Waring 1987; Henderson and Fry 1987; Pimm and Hyman 1987). These inferences can in turn provide a new perspective for fisheries management.

Comparative Lake Approach

The comparative lake approach to the study of aquatic ecosystems is based on two major premises: (1) that ecological structures and processes observed in one lake will be governed by similar processes in other lakes similar in type and (2) that comparison of lakes and their biotic communities over space and time and over a wide range of physical, chemical and climatic conditions will provide much broader insights than studies at single points in time or space (Loftus et al. 1978; Collins and Sprules 1983). Examples of the application of this approach include studies of fish production (Rawson 1952; Ryder 1965; Matuszek 1978; Schlesinger and Regier 1982), effects of perturbations (fishing, eutrophication, introductions) on salmonid communities in oligotrophic lakes (Loftus and Regier 1972), fish community structure (Johnson et al. 1977; Harvey 1978), and effects of cultural eutrophication (Schindler et al. 1973, 1980).

A major comparative lakes program in Ontario, Canada (Loftus et al. 1978), presently involves the collection of information on sets of lakes with representative fish assemblages located in various geographic regions (OMNR 1978a). Methods include monitoring of long-term trends (natural variation), experimental manipulation of communities and habitats (OMNR 1978b), and adaptive management approaches (Walters 1986). Syntheses of the resulting data sets will provide information on the structural and functional responses of fish communities over a wide range of stressed and unstressed circumstances (OMNR 1984) and will provide a means of separating the effects of specific stress factors.

Comparative lakes studies often fall within the realm of historical, descriptive science, the power of which has recently been articulated by Gould (1986) with reference to the development of evolutionary theory. The crux of the argument (in the present context) in support of historical science is that by observing lakes and communities in various states of successional development or under varying degress of stress, it should be possible to identify homologies and, hence, to trace the pathways of their succession. Description of the successional trajectories of communities should provide clues to the functional relationships underlying community organization and, in turn, to predictive theory.

Several detailed comparative studies of inland lakes presented at this symposium have described changes in fish community structure brought about by introductions of exotic species. Introduction of rainbow smelt, for example, is often followed by declining abundance of lake whitefish (Colby et al. 1987; Evans and Loftus 1987; Evans and Waring 1987) and lake

herring (*Coregonus artedii*) stocks (Colby et al. 1987; Evans and Loftus 1987). Evans and Waring (1987) reported an apparent increase in yellow perch and lake herring abundance in the presence of smelt in Lake Simcoe, however, which they attributed to possible reduced interspecific competition with lake whitefish. Colby et al. (1987) noted declines in walleye (*Stizostedion vitreum vitreum*) reproduction and recruitment following rainbow smelt introduction into inland lakes.

Minns et al. (1987) examined the changes in the fish community of the Bay of Quinte, in relation to cultural eutrophication. They concluded that nutrient additions set the general level of production but that to a major degree, species interactions may explain observed changes in the structure of the fish community. Hurley et al. (1986) speculated that interactions between walleye, white perch (*Morone americanus*), and yellow perch led to restructuring of the community when the exotic white perch population declined due to a major overwinter die-off. Their interpretation of fish community changes in the Bay of Quinte was aided by comparison with similar communities in other areas of the Great Lakes region. A critical speculation in their interpretation is that the walleye population recovered after predation on their larvae by the white perch was reduced. Similarly, Colby et al. (1987) found that the most intense fish species interactions in north-temperate lakes occurred during early life stages. They also detected a trend for radically perturbed communities to regress towards their earlier state. They warned of the lengthy periods required for such communities to reach new equilibrium and suggested that recovery sequences would be even longer in the large oligotrophic Great Lakes.

Marshall and Ryan (1987) described linkages between habitat and species assemblages by plotting their performance along select environmental gradients for a diverse set of unperturbed northwestern Ontario lakes. They found that the eight species dominating boreal forest lakes could be separated into two major groups, with similar patterns of abundance in relation to environmental clines. Walleye, northern pike, white sucker (*Catostomus commersoni*), and yellow perch form the nucleus of a percid dominated community and lake trout, lake whitefish, lake herring, and burbot (*Lota lota*) are the primary species in lake trout dominated communities. The relative importance of either group can be predicted, based on lake area, mean depth, morphoedaphic index, and Secchi transparency. Marshall and Ryan (1987) also described conditions that favor specific communities, defined in terms of terminal predators or dominant species pairs. They hypothesized that a slight perturbation may alter proportional abundances of species to a new configuration reminiscent of dominance shifts described by Skud (1982) for Atlantic herring and Atlantic mackerel (*Scomber scombrus*). Similarly, Kerr (1977) speculated that sudden transformations from one community state or domain of attraction (Peterman et al. 1979) to another might occur in percid dominated communities, due to interaction between the effects of fishing intensity and lake productivity. Fishing and productivity were identified as control variables, with percent percid composition representing the system state variable. We suggest that Kerr's analysis might apply equally well to other factors (control variables) that affect birth, death, and (or) growth rates so as to cause changes in predator–prey relationships and routes of energy flow.

Multivariate classification approach

Multivariate statistical methods provide a means of dealing with complex sets of abiotic and community variables. Three types of multivariate methods are frequently used: hierarchical classification, ordination, and discriminant analysis. Some examples of the use of these methods to classify fish communities are found in Johnson et al. (1977), Harvey (1978), Tonn and Magnuson (1982), Tonn et al. (1983), and Overholtz and Tyler (1985). Johnson et al. (1977) used discriminant analysis on 15 lake types to differentiate them on the basis of area, depth, shoreline development, water clarity, and alkalinity which were selected for analysis because they explained 90% of the variance in an earlier principal components analysis. From their analysis, it was concluded that lake depth and area were most useful in discriminating between lake types. A similar type of community analysis was also done by Tonn et al. (1983) and Tonn and Magnuson (1982). Both the Johnson et al. (1977) and Tonn et al. (1983) data sets would be amenable to a further analysis of canonical correlation.

Canonical correlation is a method for relating one set of variables, for example, species composition, with another set of variables, such as limnological characteristics. As in principal components analysis, the axes are rotated to achieve maximum variation, but in this case, the axes rotations are constrained to give the largest possible correlation between the two sets of variables. The table of canonical roots and variates helps one to decide which of the array of limnological variables best predicts the variation of species compositions (Meeter and Livingston 1978).

The analysis of cross-classified categorical data (Fienberg 1978) or multidimensional contingency tables is another multivariate method that can be employed in community studies to investigate interspecific interactions or species–habitat associations. Whittam and Siegel-Cansey (1981) used this method to quantify associations between species of birds nesting in seabird colonies, and the method appears to be a promising one for fisheries studies. This method would be particularly appropriate for a study of species compositions for data with presences or absences of species (cf. Johnson et al. 1977).

The few examples of community analyses described here are generally restricted to classifying lakes with regard to species composition and limnological characteristics or clustering groups of related species. Can these methods assist in developing an understanding of the internal rather than external factors influencing the structure of a fish community? Internal factors are exemplified by interspecific interactions expressed through predation, competition for food and space, and reproductive strategies. MacDonald and Green (1986) used discriminant analysis to study the feeding niche of five species of benthic feeding marine fish. They found that interspecific diet overlap decreased as food abundance increased. This technique could be used to compare niche separation along various niche axes within and between lakes. We suggest that more attention should be given to variables that are related to "fitness" (Gilbert et al. 1976), such as growth, fecundity, and survival. The resources required for such a study may at first appear more daunting than they actually are, but a principal component analysis will undoubtedly indicate just a few significant variables. Even supposing that there were no constraints on one's ability to describe an array of variables, can one really assign causes and effects from comparative studies? Probably not, but testable hypotheses may evolve from these analyses. However, these methods may prove equally promising in testing the results of field experiments predicated on specific hypotheses. In a related fashion, Tonn et al. (1983) have tried to predict the fish assemblages in lakes for which only a few

environmental characteristics were known. Using the discriminant function equations, they were quite successful in predicting the species composition in these lakes from environmental characters alone.

Food Web Approach

Food webs describe inter- and intraspecific interaction through predation and the exploitation of common resources. The omission of predator–prey interactions and, consequently, the assumption of constant natural mortality rate has led to inconsistencies in single-species assessment (Daan 1987). There was considerable interest in particle size distribution, or biomass spectrum models, in these proceedings. These models omit specific food web characteristics, and although the approximate levels of trophic biomass can be determined from nutrient loading, species composition, and variations in biomass around the mean, levels are strongly influenced from above by predation (McQueen et al. 1986).

Food web analyses have traditionally emphasized interactions between adult fish (larvae are usually digested too rapidly for taxonomic identification), but complete ontogenetic coverage is required if prey species can control the recruitment of a predator through predation on the latter's eggs and larvae, as hypothesized by Minns et al. (1987) for white perch on walleye, alewives on several Lake Michigan species (Eck and Wells 1987), and smelt on lake whitefish larvae (Evans and Loftus 1987). Similarly, larval food dynamics need to be investigated, as exploitation of common food resources is often greatest at this stage; Evans and Waring (1987) suggested competition between smelt and lake whitefish at age 0; Crowder et al. (1987) presented evidence that suggests that alewives may have affected survival of bloaters (*Coregonus hoyi*) and yellow perch through competition and control of zooplankton size.

Many of the papers presented during this symposium contained implicit food web models to describe or hypothesize species interactions, but it is apparent that other considerations are necessary to realize food web interactions. In Lake Huron, for example, *Mysis relicta* and *Ponteporeia hoyi* play a central role in the food web as distributors of primary production throughout the water column, while alewives intercept the vertical flow of energy, keeping it in the pelagic zone. It was hypothesized that the loss of *M. relicta* and *P. hoyi* might have led to major restructuring of the Lake Huron ecosystem. Christie (1974) employed similar considerations in suggesting that the restitution of deepwater ciscoes (*Coregonus spp.*) in Lake Ontario was necessary to improve the vectoring of deepwater components into the pelagic zone. Similarly, links between inshore and offshore communities are affected by migrations under the influence of abiotic factors. These lateral migrations would have a controlling effect on predator–prey overlaps. Thus, it is clear that food webs alone cannot be used as descriptors of community dynamics: additional data are needed to evaluate the strength of the indicated linkages. An essential data requirement is the ratio of biomass of the different food web elements. A large biomass could exert a controlling influence on a smaller biomass even when the latter was a relatively minor element in its diet, e.g. walleye on white perch in the Bay of Quinte (Minns et al. 1987).

Explicit food web models presented at ASPY were few, but covered a wide range of complexity. B. E. Skud (unpubl. data) analysed stock and recruitment relationships and found instances where the juveniles of a stock apparently buffered the young-of-the-year from predation. His concept of predation buffering supplements the more commonly applied concepts of predation and competition. A novel twist on the customary food web models was applied by Cohen and Stone (1987) and Evans and Waring (1987) in which trophic interactions were inferred through time series and correlation analyses of catch data. Kitchell and Hewett (1987) applied a bioenergetic approach to estimate the prey requirements of Pacific salmon in Lake Michigan. Pimm (1982) identified common features of food webs: number of linkages, number of trophic levels classed in one linkage, and other characteristics.

More complete food web models presented were Daan (1987) and Laevastu et al. (1982). Both models departed from the more traditional approach of computing transfer up the food chain with its requirements of poorly known transfer coefficients, and concentrated instead on calculating the size of stocks of fish necessary to support the outputs from the system and the predation by other fish. Daan's paper described an application of multispecies virtual population analysis (MSVPA) to nine North Sea fish stocks, five of which were considered to be predators. A complete set of catch data and quarterly food composition tables are required input for MSVPA. The model is run to estimate the population numbers in each cohort necessary to sustain the recorded harvest by the fishery and the estimated consumption by the five predators. Since not all species are included in the model, extra prey must be made available, and this is included under the assumption that total available prey biomass is constant and that the food intake of the five predators is constant. Vulnerabilities of each prey species to the predators were calculated so that the MSVPA could be extended to years where no stomach data were collected. The output from MSVPA is very detailed and indicated both a high variability in predation mortalities in different years (at least 40% of the mean values) and that single species VPA, because of its assumption of constant natural mortality of all age classes within a stock, produces considerable underestimates of the numbers of juveniles.

The ecosystem simulation model described by Laevastu and Bax (1986) also analyses species interactions through the food web but, instead of fitting the model to long-term catch data, defines the minimum biomass values of each species necessary to sustain the mean long-term harvests and losses due to apex predators (birds and mammals). Because all species are included in the simulation, no assumption of other prey is required and the food intake of the species is not constant but varies with season. This simulation was developed to provide first-order estimates of stock biomass when survey data and commercial catch data are unreliable and has been used to predict sustainable harvests in the Bering Sea and Gulf of Alaska and potential fishery interactions.

In the areas of their application, both of the complex food web models provided additional insights into the relative abundances of species over time. Average production of a fish species, however, might, in some cases, be independent of its trophic role in a community. For example, Kerr and Martin (1970) and Goddard et al. (1987) could find no difference in yields of lake trout between lakes where trout were planktivorous and others where they were piscivorous. Kerr and Martin attributed this to less efficient use of small particles in the shorter food chains even though the available resource was larger. Mean body size, growth rates, and age at maturity of the trout were dependent on food chain length (Martin 1966; Kerr 1979). We also caution that complex food web models have inordinate data requirements (over 54 000 stomachs were processed for 1 yr of data for

MSVPA in the North Sea); preliminary analyses and simulations are a prerequisite if an effective implementation is required.

Particle Size Approach

Particle size distribution (PS) theory is concerned with the size distributions within ecological systems, i.e. the relative frequency of size classes rather than age or taxonomic classes. Initial observations of pelagic marine communities (Sheldon and Parsons 1967; Sheldon et al. 1972) revealed that particle concentrations conform to regular patterns when grouped into logarithmic size intervals. Subsequently, similar regularities have been found for freshwater ecosystems (Sprules et al. 1983; Sprules and Munawar 1986). By regressing $\log_{10}$ biomass concentration (micrograms per litre) of various size classes of particles, divided by the weight change between size classes versus log particle weight, one can quantitatively describe the "normalized" size distribution for a particular ecosystem. The slope, intercept, and residuals can then be readily compared between systems (Sprules and Munawar 1986). The slope of the spectrum is proportional to the difference between the efficiency of converting small particles into larger ones and the exponent of the allometric relationship between body size and turnover rate (Borgmann 1982); the effects of succession or ecological stresses on conversion metabolism, predation, or life-table parameters may also be reflected by variation in the slope of the normalized curve.

In a recent reformulation of PS theory, Borgmann (1982, 1983) incorporated the concept of size-corrected biomass which, in effect, combines physiological conversion efficiency (K_1) (Paloheimo and Dickie 1966) and predator–prey size ratio into a single coefficient, the particle-size-conversion efficiency (E). Calculation of this coefficient requires a knowledge of K_1 and the body weights of predator (W_j) and prey (W_i) ($E = \log(1/K_1)/\log(W_j/W_i)$. E is then used to calculate the size-corrected biomass and, in turn, the size-corrected production. When all production at one trophic level is utilized by the next, under steady-state conditions, the size-corrected production of biomass is equivalent at all trophic levels. If the production rate at any one trophic level is known, the size-corrected production can be calculated, and the production at any other trophic level can be estimated. Estimates of fish production, calculated in this way from zooplankton production for the Laurentian Great Lakes, corresponded closely with actual historical fisheries yields, actual harvests being 21–100% of the potential yields predicted by PS theory (Borgmann et al. 1984; Leach et al. 1987). Similarly, Sheldon et al. (1977) used phytoplankton biomass and growth rate to estimate fish production for three major oceanic areas. In each case, estimates corresponded well with mean historical commercial fishery yields.

The major prerequisite condition of PS theory is that the system be in steady state (variation of biomass is stationary at each level), which implies that net reproductive rate R_0 equals 1. The assumption of steady-state conditions enables the complexity of ecosystem dynamics to be greatly reduced in PS theory. In natural systems, however, fish biomass and production vary widely on an annual basis, often by as much as an order of magnitude (Cohen and Stone 1987). These variations are caused by changes in recruitment rates, dependent on abiotic and biotic factors (Sissenwine 1984). Variations in the abundances of predators, prey (Daan 1987), and competitors (Eck and Wells 1987) might well be coherent, but they are also usually out of phase due to lags caused by different generation times (Evans and Waring 1987) or, in some cases, due to precipitous shifts in dominance (Skud 1982; Brown et al. 1987).

Fisheries managers are often concerned with determining what level of harvest is sustainable. PS theory appears to predict quite well the overall biomass and, to some extent, the slope of the normalized biomass spectrum (Minns et al. 1987). The variability around the normalized spectrum and the relative abundances of species within particle size compartments, however, is determined by intraspecific (Cohen and Stone 1987; Skud 1987) and interspecific (Crowder et al. 1987) interactions and by ecological stresses such as cultural eutrophication (Minns et al. 1987) and fishing. PS theory, therefore, provides a focus for interpretation of nutrient and predator–prey mediated structuring of fish communities, but as Minns et al. (1987) pointed out, trophic interactions and ecological perturbations must be carefully considered. Further analyses of particle size relationships are strongly encouraged, as size-specific interactions are of central importance in the transformation and storage of energy in aquatic ecosystems. Studies of energy transfer rates and efficiencies between size categories in freshwater are especially needed to better understand non-steady-state conditions.

Experimental Management Approach

The costly delays and lack of experimental control, associated with passive monitoring of natural variation (historical data), have led to an interest in experimental manipulations of communities and whole lake ecosystems (Johnson and Vallentyne 1971; Likens 1985). A key observation is that experimental manipulations require control or reference systems (comparative lakes) and long-term trend data against which the experimental results may be judged. For example, climatic or other factors may not be similar during pre- and postmanipulation periods. Management alternatives to whole system manipulations are experimental management (OMNR 1978b) and adaptive management approaches (Tyler et al. 1982; Walters 1987) in which the experimental variable is usually exploitation rates of single- or multispecies fisheries.

Perturbation experiments are of two general types (Bender et al. 1984): pulse experiments in which a sudden perturbation is applied after which the system is allowed to return to some equilibrium state (e.g. reduction in density of one or more species; Colby et al. 1987) and press experiments in which a perturbation is applied and maintained at the same level (e.g. exploitation or stocking rate). Evans and Waring (1987), for example, suggested manipulating the stocking rate of lake trout as a means of determining the optimum stock size and to regulate the structure of the fish community in Lake Simcoe. Mills and Schiavone (1982) suggested similar manipulations to regulate size structure and predator–prey balance in small lakes in New York State. They proposed the use of zooplankton size structures to assess fish community status, dominance of small-bodied zooplankton being indicative of abundant planktivores and an imbalanced fish community.

Bender et al. (1984) contrasted controlled perturbation experiments with traditional niche analysis approaches and techniques, based on natural variation in populations, to estimate species interaction coefficients. They warned that each approach has pitfalls, but that perturbation experiments are mathematically tractible and can provide information on the character and strength of species interactions. In conclusion, they recommended a pluralist approach of supplementing

ecological field experiments with as much descriptive natural history and common sense as possible.

General Discussion

Community Organization and Response

At the outset, we addressed three concerns: definition of community, functional characteristics of communities, and quantitative approaches for managing fish communities. From our review of community concepts and the empirical evidence, we conclude that a relatively broad operational definition of fish community is needed to provide a clear focus for discussion of the plethora of theories, hypotheses, and ideas about the structural and dynamic properties of animal communities. In practice, fisheries managers are now attempting to apply multispecies models, pressing the need for more quantitative ideas about the structure and function of fish communities.

Present understanding of structural characteristics of fish communities can be stated relatively briefly. Fish communities are assemblages of interacting species, which often have predictable structures associated with certain habitat types. An important question is whether fish assemblages are discrete functional units which can be managed. Clearly, fish community dynamics are dependent on other taxonomic assemblages (e.g. Hanson and Leggett 1982; McQueen et al. 1986) and the size structures of their aquatic ecosystems (particle size theory), but community structure (relative abundances of fish taxa) appears to be more dependent on fish species interactions and habitat than on trophic factors. Given these considerations, we define fish communities as coherent assemblages of interacting fish populations sharing the abiotic and biotic resources of a common environment. Coherence here refers to the dynamic partitioning of total biomass among species in a complementary manner. We wish to make it explicit, if the preceding has not already done so, that this definition of community is simply an abstraction for dealing with assemblages of fishes in practical management terms and is not intended as an absolute description of the natural world.

Functional properties of fish communities are more difficult to describe. The hierarchical size structure of fish communities is an expression of the primary functional organization of aquatic ecosystems (i.e. energy flows from the smallest to the largest particles). Indigenous fish communities are systems shaped by density-dependent species interactions, which are primarily determined by body size and other niche characteristics of coexisting species. These interactions modify species growth rates and size distributions which, in turn, influence their age-specific mortality and reproductive rates (Fig. 1) resulting in complementary species abundances. Species interactions are size dependent because of morphological constraints (mouth gape, swimming speed) and niche dependent because of species justapositioning in n-dimensional ecological space. Growth efficiency is dependent on predator–prey size ratios, prey availability, and the trophic-dynamics of capturing, handling, and processing of prey. Body size and the production–biomass relationships of fishes in any particular freshwater habitat are thereby strongly influenced by interactions among species.

Fish communities have some capacity to resist structural change and to return to a former state (structure) following disturbance. This seems especially typified by salmonid communities in oligotrophic lakes (Loftus and Regier 1972) and might be characteristic of temperate zone communities dominated by large piscivores. Resistence and resilience in these communities are founded amongst the piscivores having a dominant effect on the structure of the community (e.g. Evans and Waring 1987). Communities in temperate zone lakes not dominated by large piscivores are often dominated by stunted populations of single species (Svardson 1976). Piscivores, therefore, promote diversity in temperate fish communities by maintaining prey species at more equitable densities than would be otherwise realized. Equitability of prey species is maintained by predators switching to alternative prey as densities of prey change. Therefore, extinction of prey species is less likely because predators will not force prey densities to very low levels or permit one prey to obtain a competitive advantage of numbers.

Large body size and relatively long lifetimes are key characteristics of predators as integrators of community structure. Storage of periodic recruitment success in the adults of long-lived predators contributes to the stability of the communities that they dominate. Warner and Chesson (1985) discussed the positive influence of the storage effect on coexistence of competing species, but not explicitly with reference to the keystone predator concept (Paine 1974) or community stability. Thorp (1986), in a review of 18 case studies, concluded that predators play one of two roles in freshwater assemblages: (1) they can influence the types and numbers of species (causation of diversity) and (2) they can regulate the relative abundances of species by interrupting processes of competitive exclusion (maintenance of diversity). He suggested that predator regulation of diversity was less common than causation of diversity, but he did not specifically address the role of keystone predators on fish community structure. We suggest that regulation of diversity and stability in at least some cases is directly linked to the abundance and behavior of the keystone predator. This would occur especially in those cases in which prey switching takes place as a function of prey density.

Regulation of community diversity and possibly stability by keystone predators appears to occur in intertidal marine invertebrate communities (Paine 1974), fish communities in temperate lakes (Evans and Waring 1987), and at least one tropical reef fish community (Hixon and Brostoff 1983). In the latter example, diversity of an attached algal community was enhanced due to the influence of a territorial damselfish on the intensity of grazing by other competing herbivorous fish. Damselfish in this example influence algal diversity indirectly by competing with and spatially displacing other fish species that graze on the algae. Hypothetically, predation by a dominant piscivore might produce the same type of indirect effect on the diversity of the food resources of their prey. Indeed, piscivores are known to indirectly influence the size structures of zooplankton communities by reducing the abundance of planktivores (Mills and Schiavone 1982; Shapiro and Wright 1984). Increase in the abundance of large zooplankters in the presence of piscivores results in lower density of phytoplankton (Hurley et al. 1986; McQueen et al. 1986). Diversity changes in these cascading hierarchical systems might be due primarily to changes in equitability of species rather than to changes in species richness. In either case, the effects can be dramatic.

The devastating effect of an introduced, nonindigenous piscivore on the native fish community of Lake Gatan, Panama (Zaret and Paine 1973; Zaret 1979), illustrates that piscivores can

control the kinds of species able to survive in a habitat. Coexistence between predator and prey is presumably dependent on some compatibility achieved, perhaps, through coevolved adaptations. The concept of harmonic communities (Ryder and Kerr 1978) is an attempt to convey the idea of harmony or complementarity among coevolved species and provides an extension of the idea of a balanced community state (Anderson and Weithman 1978) to include dynamic changes over time.

Recent studies of food web structures further suggest the importance of harmonious species interactions to community stability. Field studies of a wide variety of food webs have revealed relatively constant ratios between the numbers of predator and prey species (Briand and Cohen 1984). In lakes of the unperturbed boreal forest, terminal predators contribute a near constant 50% of the total fish biomass in gillnet catches (Marshall and Ryan 1987). Jefferies and Lawton (1985) suggested that the number of types of prey determines the number of types of predators and that predators constrain the numbers of coexisting prey species. They further suggested that prey species compete for enemy-free space (Jefferies and Lawton 1985). Similarly, Holt (1984) stated that "predators may provide axes for niche differentiation among prey, just as prey, as resources, consititute niche dimensions for predators." Using a computer simulation model incorporating Lotka–Volterra predator–prey equations, Mithen and Lawton (1986) found that initial, randomly drawn assemblies of predators and prey converged to food webs with approximately constant predator–prey ratios. They concluded that competition between prey species via shared predators may be one mechanism generating constant predator–prey ratios. Enemy-free space in their conceptual model is defined in terms of niche characteristics in *n*-dimensional space. Body size, coloration, activity patterns, thermal requirements, and other habitat characteristics are examples of axes along which "competition for predators" would probably occur. Indeed, if predators facilitate coexistence, as suggested above, a type of mutualism exists between prey species and between the prey and their predators which facilitates stable population equilibria. This interplay between species in a community would appear to require considerable complementarity in the use of abiotic and biotic resources which might only come about rarely by chance alone.

Application of community concepts in fisheries management is at a relatively early stage. Consequently, most of the methods and applications discussed here are drawn from research studies describing the organization and dynamics of fish assemblages. Many qualitative hypotheses have been proposed, but development of quantitative models has been slow. Particle size theory is an exception, providing a quantitative approach for predicting the production of fish-size particles, but does not account for variation in the taxonomic structure at the fish community level. Freshwater fisheries management is primarily concerned with particular species; therefore, effective community or ecosystem models must be interpretable at the species level. This, of course, does not in any way lessen the need for community and ecosystem perspectives, but rather recognizes the level at which fisheries management resolution is required and at which management manipulation or control is generally possible.

For the management of fish populations by species to succeed, one should understand both interspecies interactions and their relationship to other biotic and abiotic components of the ecosystem. The objective of fisheries management is to maintain stable and harvestable abundances of species that are desirable in both ecological and politico–socioeconomic contexts. To do so, it is first necessary to maintain the integrity of the communities and ecosystems of which these species are a part. It follows that information is needed about both harvested and unharvested species in order to begin to understand the dynamics of these systems. Some reduction or abstraction of the full complexity is required, however, for practical reasons. Assessment costs, for example, would be prohibitive and management techniques are, in reality, limited and applicable to only a few prominent species.

Relatively few options and manipulative techniques are available to fisheries managers: (1) controlling mortality by regulating fishing (or by increasing mortality as for larval lamprey), (2) increasing recruitment directly by stocking or indirectly through habitat rehabilitation or enhancement, (3) adding new species, and (4) selective removal of species. Manipulation of system productivity by controlling nutrient inputs (LeBrasseur et al. 1978) might also be considered a fisheries management option, but is still highly experimental (Hyatt and Stockner 1985). The possible detrimental influences of excessive nutrients on fish production through changes in fish habitat quality suggest the need for an ecosystem perspective and a cautionary approach in this regard. For example, nearshore spawning habitats of fall spawner could be degraded by enhanced growth of attached algae and affects on interstitial water chemistry during the annual decomposition cycle.

Options 1–4 above are usually applied to enhance single-species but, in most cases heretofore, have had unanticipated effects on other species. Fisheries managers seek to explain the species interactions underlying these responses and to predict community responses to changing species mortality and recruitment rates resulting from either natural variation or ecosystem manipulations by humans. A critical problem arises in assessing community state and monitoring changes. Managers need to know what constitutes an adequate quantitative model for assessing changes in the dynamics of managed fish communities.

A definitive answer to the above question is not available, but evaluation of community structures in north-temperate lakes suggests that relatively few species tend to dominate these assemblages (Marshall and Ryan 1987) and that changes in their relative abundances, size and age distributions, or mortality rates should provide an indication of any major shift in structure (Colby 1984). Many fish assemblages are dominated by keystone predators, and these species alone might provide a primary indicator of community stability (e.g. Ryder and Edwards 1985; Evans and Waring 1987). Application of actively adaptive management strategies (Walters 1986, 1987) would be a feasible way of testing the keystone predator hypothesis, since most fisheries concentrate on harvesting these species, making them susceptible to manipulation. Heavy exploitation, if selective for large fish, however, would effectively eliminate the storage capacity of the long-lived species (Warner and Chesson 1985), thereby stripping away an integral part of their life history, not only jeopardizing their role in the community but also their long-term prospects for survival. The storage effect (Warner and Chesson 1985) renders the adult stocks of these relatively long-lived species temporally unresponsive to environmental change. Because of the capacity to accommodate variable recruitment in these species, even the early life stages may be too variable to serve as an effective indicator of community change. The present hierarchical model

of cascading trophic effects (McQueen et al. 1986) provides the basis for an alternative, but considerably more complex, multifunction model from which fish and nonfish species could be selected on the basis of their trophic roles and response times to assess the state of an aquatic ecosystem.

Ecological Scale and Management Perspective

Choosing the appropriate spatial and temporal perspective is essential to the process of assessing the status of fish communities for management. For example, bays and estuaries are often only exploited seasonally by some species, but they can be essential to the completion of the life cycle of those species, and hence have a critical influence on the transfer of energy and on system dynamics much further afield. Also at a given time, communities and ecosystems may appear to be in dynamic equilibrium but, viewed over very long periods, stability becomes more difficult to define, both in terms of stochastic variation and successional change. In the following discussion, we use the term succession in the broad sense of ecosystem development (Odum 1969). Succession provides a unifying theme for consideration of directional changes in complexity, diversity, connectance, and variability in fish communities. In contrast, the equilibrium view is simply a convenient and practical way of abstracting the dynamic temporal complexity of ecological systems.

Holling (1985) suggested that the appropriate spatial scale is defined by the most mobile of the key biological variables in a community. The relevant spatial scale of a lake trout dominated community, for example, might therefore extend over several hundred kilometres (Eschmeyer et al. 1953). Similarly, Holling suggested that the relevant temporal scale is a small multiple of the longest lived key biological variable. Again, lake trout would set the scale, having a maximum longevity in the order of three to four decades (Healey 1978). In the boreal forest, however, black spruce trees (*Picea mariana*) are coupled to lake trout dynamics through effects on hydrology, nutrients and minerals (Ryder and Edwards 1985, p. 82). Inclusion of black spruce forest as part of the lake trout system would extend the relevant temporal scale to 100 yr or more. These scales are much greater than usual management perspectives, but arguably represent the appropriate focus for defining the bounds of these systems (Holling 1985). Changes in fish communities of the Laurentian Great Lakes during the present century provide direct evidence of the relevance of these scales for management (Christie 1974; Christie et al. 1987b).

Management of freshwater ecosystems, in general, can benefit from even broader perspectives. Applying the comparative lakes approach and the concept of homologous processes from our earlier discussion, images of the successional trajectories of fish communities can be reconstructed. Cognizance of the successional development of a community is valuable to management because associated changes in fish body size can be related to variability and productivity. Also, various anthropogenic factors might operate to modify successional development in predictable ways (Odum 1985). For example, a stress which leads to the loss of a dominant large piscivore theoretically would be expected to result in increased total productivity (Fenchel 1974; Dickie 1976; Adams 1980; Banse and Mosher 1980), but also increased variability, smaller mean body size, and possibly lower economic value to a multispecies fishery. Earlier, we showed how body size and growth rate influence various metabolic, behavioral, and life history parameters thereby coupling species interactions and population dynamics (Fig. 1). The linkage between those relationships and several community properties during successional development are seen in Fig. 2:

(1) As successional development proceeds, average size of species in the fish community increases (Fig. 2A) given sequential invasions of, initially, small, short-lived species and, later, large, long-lived species.

(2) As average size increases, reflecting a change in the ratio of predators to prey, diversity will increase (Fig. 2B). Further increases in diversity would be due to increased evenness as the community becomes dominated by a few large predators. Diversity may eventually decline as successional changes result in loss of environmental heterogeneity.

(3) Community mortality rate (Z_c) declines with increase in average size and longevity as long-lived species begin to dominate (Fig. 2C). Variability also declines as size increases, due to the storage effect of increased longevity.

(4) Total fish production will increase as diversity increases during succession, due to increased exploitation of available habitats and associated resources. Trophodynamic theory predicts, however, that as larger species begin to dominate and food chains become longer, total production will decline (Fig. 2D).

If fishery yield increases as production increases, mature communities dominated by large *K*-adapted predators will provide smaller yields than earlier successional stages (Fig. 2D). Regier and Henderson (1973) postulated this relationship more than a decade ago, and also speculated that economic returns would be maximized in an opportunistic multispecies commercial fishery at an intermediate successional level above that producing maximum biomass yield, but well below the mature state. These relationships would be dramatically different for large recreational fisheries where the catchability and economic value of large predators would greatly exceed that of smaller -*r*-adapted species. Maximum economic benefit would probably occur at the mature successional stage, well beyond the point of maximum fish biomass production. Reduced variability of the mature successional stage, due to integrative and governing effects of species interactions, suggests that mixed recreational and commercial fisheries might also be best managed at the mature state, but below the level at which diversity begins to decline.

The relationship between successional stage and average body size links the hierarchical size structure of fish communities to production and yield through size-linked species interactions. Factors that influence species interactions, therefore, by altering growth and net productive rate can influence the successional trajectory and production and yield characteristics of fish communities. A major challenge is to manage fish communities to optimize their productivity and variance characteristics while minimizing changes in the corresponding successional state.

Predicting Responses of Stressed Fish Communities

Attempts to explain changes in the composition of fish communities as in the Laurentian Great Lakes have been confounded by the simultaneous actions of factors such as nutrient enrichment, fishing, and species introductions. Loftus and Regier (1972), reviewing the proceedings of the SCOL Symposium, concluded that until one can partition the influence of these factors on the fish community, the efficiency of various

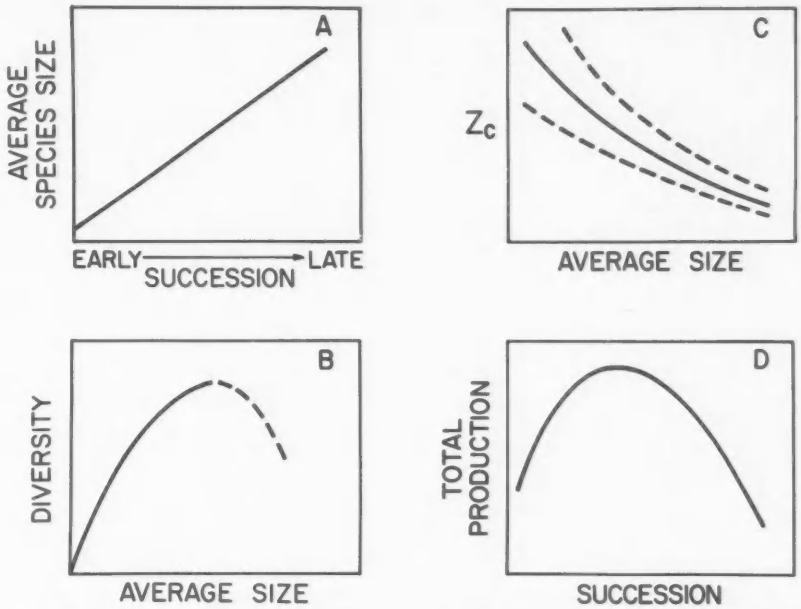

FIG. 2. Postulated trends relating various fish community parameters and either (A and D) successional stage or (B and C) average fish body size. In Fig. 2C, Z_c is the weighted (by numerical abundance) mean community mortality rate; the broken limits indicate variation in Z_c. In Fig. 2D, succession progresses as in Fig. 2A.

management practices will remain unclear. In this section, we examine the effects of nutrient enrichment, fishing, species introductions, and interactions among these factors on size distributions in a fish community to see if the effects can be better understood in terms of size-linked community interactions.

Nutrient enrichment

Nutrient enrichment will, in most situations, result in increased primary production. Changes in species composition of the phytoplankton are less predictable, but barring extreme shifts to blue-green algae or oppositely to nanoplankton dominance, nutrient additions will result in increased secondary production and, in turn, to changes in fish production (Hyatt and Stockner 1985). Fish responses may be of at least two types mediated through quite different processes. If food abundance changes but habitat quality does not, increased growth rates, earlier maturation, and increased production would be expected (e.g. Svardson and Molin 1981; Hyatt and Stockner 1985). The effects, as discussed, can change species demographic variables and influence interactions between species, thereby causing major shifts in species abundance. Time spent at various ontogenetic stages and reduced vulnerability to starvation (larvae) and to predation (juveniles) would be the primary mechanisms (Crowder et al. 1987). These effects would be accentuated if warm- and cool-water species respond differentially (Svardson and Molin 1981).

A second mechanism might involve habitat degradation and reduced survival of the more sensitive species (e.g. salmonids), resulting in decline in their abundance. If the most sensitive species is also a top piscivore, dramatic shifts in dominance towards increased abundance of small prey species and possibly some benthivores would be expected (Hurley 1986; Minns et al. 1987). An increase in planktivores would result in a reduction in large zooplankton and a further increase in algae. Other factors affecting the abundance of piscivores (e.g. fishing) would have a similar synergistic effect on algal biomass. Predicting the actual species shifts should be possible given a knowledge of the environmental requirements and predator–prey and competitive relationships for the prominent species.

Fishing

The first effect of excessive fishing on a fish community is to inflict increased and differential mortality. Consequently, the average size of the population is reduced, even if within the remaining size classes the growth rate is improved as a result of reduced intraspecific competition. The consequences of this change in the size distribution are similar to those described in the previous section. The reduced size distribution results in fewer cohorts comprising the spawning stock, which increases the risk of collapse of the stock (Murphy 1967) and community transformation (Kerr 1977). A change in the size distribution will also result in a change in the sizes of prey taken and, in addition, a new range of potential predators. A particularly good example of the consequences of size-selective fishing is found in lake trout in Lake Huron. The intense commercial fishery reduced the size distribution of trout so that when lamprey parasitism increased, the size classes of trout that were extant were more likely to die as a consesequence of parasitism (Christie 1972, 1974). The larger trout that could withstand multiple attacks were selectively removed by the fishery. The loss of this "buffering" stock of reproductively important fish was a contributing factor in the decline of lake trout.

The loss or reduction of species through selective fishing

further exacerbates the change in size distribution of the community, resulting in new rates and directions of energy transfer (Eck and Wells 1987). In many cases, the rates are increased in directions that do not result in the most desirable use of the potential energy, and in some cases, energy sinks might occur in which biomass is locked up in undesirable sizes or species (e.g. Johnson 1977; Hanson et al. 1983). The severity of the effects of fishing would depend, in part, on the fishing effort, the species caught (target and incidental), and initial community structure. The general effect of fishing could be a higher but more variable production.

Species introductions

The effect and success of an exotic species will depend largely on its size distribution in relation to its prey and corresponding predators. One assumes that the physical and chemical conditions do not prevent recruitment. When the sizes of exotic versus indigenous predators are similar, and abundant prey are available to both, the success of the exotic will depend on the reproductive success of the exotic relative to other predators. In considering the ratios of size for the exotic predator to indigenous predators, one must take into account the range of values observed for the exotic in its natural environment. The more plastic the phenotype of the exotic, the greater is its chance of success, in most cases. This is not to suggest that exotics always have greater fitness than members of an existing community, but rather that they must possess a certain minimum fitness for colonization of the new habitat. Invasibility of new habitat by an exotic might be more directly related to the predisposition of the habitat to invasion due to prior disruption of the existing fish community by exogenous stresses (Christie et al. 1972). The preceding arguments apply mostly to predators not themselves subject to much predation. An important consideration for other species is their size in relation to potential predators. The most successful fish of this sort is one with a relatively high reproductive value and profitable ratio of its size to available prey, as well as a size in relation to its predators that makes it an unprofitable species for coexisting predators. The successful exotic, therefore, will survive by securing a portion of the energy available by either utilizing a unique distribution of prey or successfully sharing a common prey while escaping the depredations of existing predators, or simply by displacing a potential competitor by its fitness.

Is it worthwhile to attempt to partition the effects of each of the major stresses (nutrient enrichment, fishing, and species introductions), and if so, how does one do it? The answer may depend on the circumstances. The analytical approach for determining a prescription for rehabilitation is different from predicting the consequences of one of the stresses on an unperturbed system. In most cases, one must deal with a community that has been affected by several stresses that can produce the same effect, singly or in concert with the other stresses. In theory, one could subdivide communities into (a) nutrient enriched, (b) fished, and (c) exotics introduced. By comparing the mean size of selected species or the whole community when the stresses act alone (a, b, c) or in combination (ab, ac, abc, etc.), one could partition the variance due to treatments, additive effects, and interactions. However, in practice, it may well prove difficult, if not impossible. Interactions of this type have highlighted the need for community and ecosystem models. For example, interactions between eutrophication effects and an introduction (rainbow smelt) in Lake Simcoe appear to have resulted in major restructuring of the fish community (Evans and Waring 1987), interaction between fishing, exotic fishes (salmonids, alewives), and eutrophication in Lake Michigan has resulted in reduction in algal biomass (Scavia et al. 1986) and changes in the abundances of indigenous fishes (Jude and Tesar 1985; Evans 1986), and similarly, interaction between eutrophication and an exotic (white perch) in the Bay of Quinte appears to have resulted in changes in zooplankton species composition, and effects on phytoplankton are expected in the near future (Hurley et al. 1986). These results suggest that assessment models will need to include several trophic levels and that information about species size relationships and niche characteristics will be needed to separate and predict responses (Minns et al. 1987).

Prediction of the effects of a new stress on a previously unperturbed or partially disturbed community might be possible if one was cognizant of the size ratios, niche characteristics, and life table parameters of the relevant species. In the same way, it might be possible to predict the influence of invading species or to identify potential invaders by comparing their sizes, niche characteristics, and life table parameters with those of the indigenous species. Retrospective analyses of known case histories would be useful to see if the success of established exotic species can be explained in these terms.

Management Applications

Freshwater fisheries managers must understand fish community structure and dynamics to sustain optimal fishery yields, especially for species which are nonterminal predators in their food webs. Fish communities are not just aggregations of species, but rather highly dynamic, interactive subcomponents of aquatic ecosystems. One important feature of these systems is their hierarchical size distribution, which ranges from unicellular bacteria and algae to fish, spanning several orders of magnitude. The concept of hierarchical organization (O'Neill et al. 1986) provides a very useful model for analysing the structure and dynamics of fish-producing systems and of interpreting organizational changes. Size-dependent predation and other process rates, for example, are important to the organization of freshwater fish communities; large indigenous piscivores can maintain a stable abundance of smaller, shorter-lived prey species. Optimal foraging theory predicts that prey switching by large piscivores will occur when it becomes energetically profitable. Switching of lake trout from yellow perch to introduced lake herring (Martin and Fry 1972) or from lake herring and other indigenous prey to more abundant introduced rainbow smelt (Evans and Loftus 1987) are examples of this type of prey switching. A mechanism, therefore, appears to exist by which piscivores can regulate prey abundance throughout the community, without eliminating any single prey species while at the same time fostering their coexistence.

Growth rate and body size of both predators and prey can greatly affect the dynamics of their populations. Predation among fishes is usually limited by the size of the mouth gape, and therefore, vulnerability of prey is related to body size as is the efficiency of predation. Competition effects might also be size dependent; usually, species of very similar sizes are thought to be most likely to compete. Of course, morphology as well as size can have important effects on feeding efficiency. A further complication is that an adult predator (lake trout) might eat prey (lake herring or rainbow smelt) that earlier compete with or eat

their young. Ontogenetic shifts in feeding behaviour (Crowder et al. 1987) need to be carefully considered, particularly with reference to introduced exotic species. Growth rate in the lake trout example would influence the duration of time that their young would be vulnerable to competition and (or) predation. Werner and Gilliam (1984) explained how this vulnerability is directly linked to food availability, growth rate, and mortality.

At this time, community ecologists have many hypotheses, but few definitive answers; however, several key characteristics of fish communities that were discussed at the ASPY Symposium are immediately relevant to management concerns:

(1) The productivity of fish communities is primarily controlled by energy inputs, nutrients, edaphic factors, and habitat variables, but the distribution of the production by species is strongly influenced by size-dependent interactions between species usually involving the young of one of the interacting species.

(2) Large piscivores have a stabilizing influence on the abundances of their prey and associated species due to their longevity and storage of periodic strong recruitment; their reduction or loss can result in density-dependent changes in growth rates and abundances of the remaining species; manipulation of the density of large piscivores appears to provide one effective way of managing community structure.

(3) The number and relative proportions of species are also strongly influenced by habitat (e.g. lake area, mean depth, thermal characteristics), suggesting the importance of environmental heterogeneity; availability and distribution of habitable space may influence the intensity of species interactions resulting in variation in the expression of community structure (Henderson and Fry 1987); integrity of the early life habitats is especially important and they may be located remote from the adult habitat.

(4) Exotic species usually have a disruptive effect on community structure; introductions, therefore, should be restricted to species that are otherwise closely associated with the local indigenous fauna (Ryder and Kerr 1984).

(5) Anthropogenic factors (e.g. fishing, eutrophication) act on fish communities by disrupting their size- and niche-structured organization.

(6) Fish community dynamics are bounded by spatial and temporal scales set by the most mobile and longest-lived dominant species (Holling 1985).

(7) Successional processes appear to strongly influence fish community diversity, productivity, and stability through body size linked characteristics of species.

(8) Fish communities can be managed as relatively discrete functional units, but dependency on whole system dynamics ultimately necessitates an ecosystem perspective.

(9) Some indicators of structural transformation in fish communities are changes in algal biomass (Shapiro and Wright 1984), zooplankton community structure (Evans 1986), fish diets, fish growth rates, size distributions and species abundances, especially of large piscivores, measures of community complexity (Hurley et al. 1986), and short-term measures of variability in fish abundance (Pimm and Hyman 1987).

Application of community concepts in fisheries management to date has involved incorporation of predator–prey interactions of exploited species in the sea (e.g. Anderson and Ursin 1977; Laevastu and Larkins 1981; Daan 1987) and manipulation of predator–prey balance in freshwater ponds and lakes (e.g. Anderson and Weithman 1978). Both applications have clearly verified the influence of species interactions on species mortality rates and community structure, but both also continue to be experimental. MSVPA models (Daan 1987), which incorporate predator–prey information to account for variation in natural mortality, were designed to extend conventional VPA based on exploitation mortality estimated from catch statistics. These and similar models represent the first major attempt to incorporate community interactions in a quantitative way to estimate fish mortalities and abundances, but have proven to be extremely data intensive and limited to areas where reliable and detailed catch statistics are available for the major predators and their primary prey. Whether it is feasible to pursue this type of data intensive approach appears to be a valid concern.

Walters (1986, 1987) argued that within the context of fisheries management, an adaptive approach is the one of choice given the uncertainties of ecological and politico–socioeconomic systems. He advocated active rather than passive (natural variation and management mistakes) adaptive experiments to learn, through experience, the dynamic relationships among regulating variables. We conclude that deliberate management manipulation of fish communities, while applying past experience and existing ecological knowledge to make the management choices, offers a realistic means of testing qualitative ideas about system responses and of acquiring new knowledge in a timely way. Thus, we would agree with Walters to the extent that adaptive experiments can be focused on sound hypotheses generated from descriptive, comparative and experimental science.

Management experiments need to be much more than trial and error manipulations. The importance of species interactions is certain and decisions need to include consideration of predator–prey and possible competitive relationships, based on life history and niche characteristics. We have attempted to identify key functional relationships underlying community dynamics and to identify information relevant to management of fish communities. While quantitative theory is at an early stage of development, it is clear that existing qualitative knowledge can be invaluable in making management choices and, further, that experimental and adaptive management can become powerful tools in testing and developing new theories about how fish communities operate.

Research Needs

The ASPY Symposium has helped consolidate the idea that an ecosystem perspective is required to fully comprehend the dynamics of fish-producing systems. We suggest the application of hierarchical analysis to identify the key functional relationships governing fish production and organizational structure. This approach facilitates the identification of important habitat and niche variables and the corresponding physiological and behavioral responses that modify body size and associated tropho–dynamic relationships between species. Hierarchical analysis can also help to isolate the levels of organization at which various external or internal processes influence the dynamics of the system (Kerr 1982). Thus, while it appears to be possible to manage fisheries at the level of community, it is clear that full understanding of community dynamics will require a broader, ecosystem perspective. Allen (1985) noted the need for descriptive studies during the early stages of any science. This is especially relevant to fisheries ecology where predator–prey relationships for all life stages are rarely known for even the major species. Development of new understanding

of fish communities, therefore, will require an interactive process of external and internal analysis at each level of the trophic size hierarchy, using scales of space and time appropriate to the natural processes. With this in mind, we suggest several aspects of fisheries ecology that require additional research: (1) the relationship between successional status and stability characteristics of fish communities (Odum 1969; Pimm and Hyman 1987); Christie et al. (1987b); (2) the effects of species depletion (fishing) and loss on fish community structure, susceptibility to transformation, and reversibility of these processes (Kerr 1977; Pimm and Hyman 1987); (3) the direction and magnitude of species interactions (predation and competition), particularly those associated with early life history and ontogenetic change (Christie et al. 1987a; Cohen and Stone 1987; Colby et al. 1987; Evans and Loftus 1987; Evans and Waring 1987; Henderson and Fry 1987; Le Cren 1987), and their influence in the propagation of effects either up or down the trophic hierarchy of aquatic ecosystems (McQueen et al. 1986); (4) the relationship between species habitat requirements and fish community structure (Tonn and Magnuson 1982; Tonn et al. 1983; Marshall and Ryan 1987); (5) the effects of ontogenetic changes and associated species interactions on life history parameters (growth, mortality, reproductive rates); this will require experimental studies and further development of models that extend PS theory (size-linked energy transfer efficiency and storage) to include time-variant processes as well as steady states (Werner and Gilliam 1984; Borgmann 1987; Daan 1987; Dickie et al. 1987; Minns et al. 1987); (6) the effects of the major ecological stressors (fishing, eutrophication, contaminants) and interactions among stressors on size-linked species interactions, fish community structure, stability, and productivity (Pimm and Hyman 1987); (7) the expansion of comparative (spatial and temporal designs) and manipulation approaches in small inland lakes (OMNR 1978a, 1978b; Cohen and Stone 1987; Colby et al. 1987; Evans and Waring 1987; Henderson and Fry 1987; Marshall and Ryan 1987) to develop a better understanding of species habitat requirements and niche interactions; and (8) the development of improved, unbiased methods for assessing fish community composition and species abundances.

These aspects of fish community dynamics all arise from the need to understand the nature of the functional relationships that regulate community structure and productivity. They can be summarized in the following three questions: (1) what is the present structural state of the community? (2) what minimal set of variables can be used to characterize the state of the community at time t? (3) what are the critical inputs and functional relationships between the individual species and their abiotic and biotic environment that cause the community to change from one state to another?

These questions, which borrow from the systems approach (Odum et al. 1979), suggest a conceptual focus for fish community studies that has often been missing. The approaches that we have outlined, descriptive studies (ontogeny, food webs, species interactions), analytical studies (trend-through-time variation, size and diet effects on growth efficiency and energy transfer and storage, relationships between growth, size, and life history parameters), and modelling approaches (food web based production models, size-structured multispecies fisheries assessment and yield models), represent a complex array of interests which requires focusing if significant fisheries applications are to be achieved in a timely manner. We suggest that hierarchical analysis provides a promising function-oriented approach for achieving this focus.

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A Review of Methods for Prediction of Potential Fish Production with Application to the Great Lakes and Lake Winnipeg[1]

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Methods for estimating fish production in aquatic ecosystems range from simple empirically derived estimators, such as morphoedaphic indices, to complex ecosystem simulation models. As first-order estimators, the former are attractive to managers because they are simple and relatively inexpensive to apply and interpret. Application of the latter group has been limited because many of the data inputs are difficult and expensive to obtain. Between these extremes are several models, such as the biomass – size spectrum model, that provide useful information for moderate expenditures of time and effort. Existing and new methods are reviewed in the light of production theory and several are applied to Great Lakes and Lake Winnipeg data. Eight empirical models derived from limnological variables were selected from the literature and used to estimate potential fish yield for the Great Lakes and Lake Winnipeg. The models predicted a fairly narrow range of potential yields, but when compared with historic yields, none was consistent for all lakes. The best overall empirically derived estimator of potential yield in the Great Lakes was the morphoedaphic index. Potential fish production estimated from invertebrate production with Borgmann's biomass – size spectrum model was considerably greater than historic yields or the yield estimates from the empirical models. In a third approach, we calculated life history parameters for "small" and "large" fish in the Great Lakes and combined these with Borgmann's production model, empirical information on population production/biomass ratios from the literature, and classical population dynamics theory to estimate potential production and optimum sustained yield for each group. Historic sustained yield, as a percentage of optimum sustained yield, varied from a low of 6 for "small" Lake Ontario fish to 100 for "large" Lake Erie fish.

Les méthodes d'estimation de la production piscicole dans les écosystèmes aquatiques vont de simples estimateurs empiriquement dérivés comme les indices morphoédaphiques à des modèles complexes de simulation d'écosystème. En tant qu'estimateurs de premier ordre, les premiers sont intéressants pour les gestionnaires parce qu'ils sont simples et relativement peu coûteux à appliquer et à interpréter. Par contre, l'application de modèles a été limitée parce qu'un grand nombre des données nécessaires sont dispendieuses et difficiles à obtenir. Entre ces deux extrêmes, il existe plusieurs modèles comme le modèle de la gamme de la taille de la biomasse qui fournissent de l'information utile avec des dépenses modérées de temps et d'effort. On présente les méthodes actuelles et de nouvelles méthodes à la lumière de la théorie de la productivité et on applique plusieurs de ces méthodes à des données recueillies dans les Grands Lacs et le lac Winnipeg. On a choisi dans les ouvrages publiés huit modèles empiriques tirés de variables limnologiques; ils servent à déterminer le rendement potentiel en poissons des Grands Lacs et du lac Winnipeg. Les modèles prédisent une gamme assez petite de rendements potentiels; toutefois, une

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comparaison de ceux-ci avec les rendements historiques a révélé qu'ils n'étaient pas uniformes dans tous les lacs. Dans les Grands Lacs, le meilleur estimateur général du rendement potentiel dérivé empiriquement s'est révélé être l'indice morphoédaphique. La production piscicole potentielle calculée d'après la production d'invertébrés à l'aide du modèle de la gamme de la taille de la biomasse de Borgmann était nettement plus élevée que les rendements historiques ou les estimations du rendement obtenues des modèles empiriques. Dans une troisième approche, on a calculé pour de «petits» et «gros» poissons des Grands Lacs des paramètres du cycle vital qui ont été combinés avec le modèle de production de Borgmann, des données empiriques sur les rapports démographiques production/biomasse tirées d'ouvrages publiés et la théorie classique de la démécologie pour estimer la production potentielle et le rendement soutenu optimum pour chaque groupe. Le rendement soutenu historique, exprimé en pourcentage du rendement soutenu optimum, a varié d'une faible valeur de six pour les «petits» poissons du lac Ontario à une valeur élevée de 100 pour les «gros» poissons du lac Érié.

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Ecological theory has led to the development of many methods for the estimation of potential fish production in marine and freshwater ecosystems. Methods range from simple empirically derived indices of production to comprehensive ecosystem simulation models. From the management view, two main attributes of useful models are simplicity and accuracy. Existing models vary in their ability to match both of these characteristics. Therefore, model selection often requires definition of the balance between simplicity and accuracy which is appropriate for the specific management problem at hand.

The ASPY Symposium provided an opportunity for a discussion of production theory and a review of existing methodology for estimating fish production and yield. This process led to the development of new ideas and techniques which we believe could be tested with existing data sets from the Great Lakes and elsewhere.

Our objectives in this paper are (1) to review existing methodology and to describe new techniques for the estimation of potential fish production in the light of production theory and (2) to apply and compare several of these approaches to estimate potential fish production of the Great Lakes and Lake Winnipeg.

Production Theory and Methodology

Definition of Production

Thienemann (1931) defined production as the sum of growth increments of the individuals of a species population, both survivors and nonsurvivors, through a discrete time period. We define production (P) simply as the elaboration of new biomass (B) from the existing standing stock. P/B therefore defines the growth rate (somatic growth plus reproduction) of the identified biomass. Calculations are usually made for particular species or groups of species within a class and may be summed in various ways to approach a "total" production.

In estimating fish production from yield data, we generally deal with annual time periods and either initial or average biomass during the period. In the present discussion, production is expressed in terms of weight rather than numbers.

Uses of Production Measurement

Within the ASPY context, production may be measured for the following.

1. Estimation of potential yield

Data on total production of a specified class of animals in a body of water provide one measure of its potential yield.

2. Indication of system change

Estimates or indices of production for total systems, or some selected parts of them, may be better indicators of system change than the more frequently used indices of population density (e.g. catch per unit of effort) or yield. Changes in production resulting from fishing, eutrophication, contaminants, or particular species association provide measures of the effects of these factors on the ecosystem as a whole.

3. Water quality management

Production ratios provide a comprehensive measure of water quality and therefore can be used to detect and track biologically significant changes in the aquatic environment.

Methods of Estimating Production: Review and Issues Arising in Application

1. Empirically derived indicators

Many attributes of aquatic systems have been used to develop simple estimators of fish production. Some are included in the following classification.

(a) Morphological – Area, volume, depth, or volume/area of whole lakes or of stratified layers; ratios of epilimnion to hypolimnion, mixed layer depths, rates of exchange, or flow-through.

(b) Physical and chemical — Nutrient concentration, dissolved gases, transparency, total dissolved solids (TDS), temperature.

(c) Biological — Chlorophyll *a* or other pigment concentration, particulate organic matter (POM), living organic matter (ATP fractions of POM), dissolved organic matter (DOM), indices of diversity or community structure.

(d) Derived ratios — Various ratios are derived from combinations of morphological and other indicators into what is referred to as morphoedaphic indices (MEI).

Since Ryder's (1965) landmark paper there has been extensive use of MEI in addition to other physical, chemical, and biological indices. In general, such indices are designed for simplicity of application. They treat yield of fish as a "shadow" statistic representing fish production. This embodies the implicit assumption that the yield for a given lake represents the same fraction of total production as the yields for the other lakes with which it is to be compared. Where reliable and comparable

TABLE 1. Empirical predictors of fish yield in temperate lakes with relevant references to methodology for estimating total yield and species yield.

Variable	Total yield	Species yield
MEI	Ryder 1965 Ryder et al. 1974 Ryder 1982 Jenkins 1982 reservoir/ sportfish	Jenkins 1982 (smallmouth bass)
Total phosphorus	Hanson and Leggett 1982 Ryan 1980	
Primary production	Liang et al. 1981 McConnell et al. 1977 Oglesby 1977	
Algal biomass (chlorophyll *a*)	Jones and Hoyer 1982 (sportfish) Oglesby 1977	Oglesby et al. 1987 (walleye)
Macrobenthos	Matuszek 1978 Hanson and Leggett 1982	Matuszek 1978 (lake trout, lake whitefish, walleye, sauger)
Climate	Schlesinger and Regier 1982 Schlesinger and McCombie 1983	Schlesinger and Regier 1982 (lake whitefish, northern pike) Jenkins 1982 (northern pike) Schlesinger and McCombie 1983 (walleye)
Effort	Schlesinger and McCombie 1983	Schlesinger and McCombie 1983 (lake trout, smallmouth bass, walleye) Goddard et al. 1987 (+area)
Morphometry	Schlesinger and McCombie 1983 Youngs and Heimbuch 1982 (area) Rawson 1952 ($\bar{z}$)	Goddard et al. 1987 (+effort)

measures of fishing effort are available, this assumption can be validated by comparing the intensity of effort (e.g. effort per unit area) across lakes. If significantly different levels of effort exist, then separate regression analyses must be done within each effort level. Alternatively, analysis of covariance can be used, with effort as a covariate (see Goddard et al. 1987). Thus, in yield-based regression equations, the apparent performance of limnological indicators depends primarily on two factors: the suitability of the indicator as an independent variable and the underlying (and unknown) relationship between yield and production in the specific set of lakes studied.

A representative set of those indicators that have been tested is listed in Table 1. Where comparisons have been made, such variables as total phosphorus concentration (Hanson and Leggett 1982), primary production (Oglesby 1977), and macrobenthos (Matuszek 1978) have been found in specific instances to constitute improved indicators over the original MEI defined by Ryder (1965) (total dissolved solids/average depth). Ryder et al. (1974) have suggested alternative definitions of the index and expected conversion factors. Oglesby (1982) has reviewed earlier applications.

Limnological indices of fish yield are an important source of first-order predictions when little other information is available. They are among the first exploratory tools to be used in the evaluation of the relationship between fish production and exploitation. Therefore it is critical to the increased use of these indices that studies be directed to developing relatively homogeneous lake data sets wherein the yield and limnological variables are measured and the relationships defined.

2. Comprehensive methods

(a) Biomass – size spectrum models — Production models based on the biomass – size spectrum (first defined by Sheldon et al. 1972) depend essentially on the assumption that biomass is relatively stable across a logarithmic scale of particle mass in pelagic ecosystems (Platt and Denman 1978; Sprules and Munawar 1986). The simplest direct use of this model is to predict fish biomass (and thence production) from an estimate of algal or zooplankton biomass. This underlying empirical regularity in ecosystem structure can be explained by a steady-state bioenergetic theory developed in detail by Kerr (1974) and Sheldon et al. (1977).

Applied spectrum analyses are of two types: those that examine the "coarse" structure from microorganisms to top predators and those that examine the "fine" structure over what is normally one or two trophic levels.

The coarse structure of the spectrum is a function of organism bioenergetics and predator–prey relationships and may be

applicable where there are relatively few data (i.e. particle-size-conversion efficiency, ϵ, and the relationship between turnover rate and body size). Models of this type can provide estimates of potential production for the entire community over various size classes and have been so applied to Lake Ontario (Borgmann 1982, 1985; Minns et al. 1987).

The fine structure of the spectrum has been addressed by Dickie et al. (1987) who noted regularities in weight-dependent P/B ratios per unit area of habitat within organism groupings (e.g. fish). The more detailed spectral structure appears to reflect ecological costs of assimilation and predation above and beyond simple respiration costs. They illustrate the utility of this refinement through analysis of Atlantic cod (*Gadus morhua*) and Atlantic herring (*Clupea harengus harengus*) yields.

J. E. Beyer's (unpubl. data) dynamical form of the model addresses fine-scale structure through weight-dependent specific growth and mortality parameters that can change with time.

The originally meagre data base on fine-scale structure has been expanded for plankton by Sprules et al. (1983) who noted that aquatic ecosystems tend to fall into homogeneous subgroupings in terms of spectrum characteristics (Sprules and Munawar 1986).

In fisheries analysis it should be recognized that the biomass spectrum model deals only with total biomass or production at average body sizes. There is no breakdown into species if they are approximately the same sizes. In the Great Lakes context, other information such as the traditional catch series or single-species model is required to carry out such partitioning (Loftus et al. 1987). On the other hand, biomass models may offer the advantage that unique diagnostic features of whole systems may be defined which permit their characterization and identification into types, providing a classification not possible from traditional dynamic models (Sprules and Munawar 1986). Within these subgroups, partitioning the expected production amongst species may be feasible.

There is also evidence (Schwinghamer 1985; Sprules et al. 1983) that fine spectrum characteristics are indicative of close coupling or biomass exchange between benthic and pelagic communities. This could help to identify situations in the Great Lakes where production of a pelagic stock is dependent on benthic (or littoral) processes.

In theory, steady-state conditions in a pelagic community produce a linear and flat biomass spectrum on a coarse scale. Deviations from this condition, or more careful analyses of fine-scale structure and its variability, would measure overall community perturbations and could provide some warning of impending catastrophic changes in system behaviour due to anthropogenic stresses. Because recent changes in Lake Michigan fish and plankton communities are reasonably well documented, retrospective examination of concurrent changes in the size spectrum would help assess its utility in representing and characterizing a system in flux.

With the biomass spectrum, we are working on a continuum of trade-off between precision and complexity and cost of data. It could be that the two extremes are represented by the original empirical model (low-cost data, low precision) and Beyer's dynamic model (high-cost data, high precision), with intermediate points on the continuum occupied by the approaches of Borgmann (1987), Sprules and Munawar (1986), and Dickie et al. (1987). Further study of these approaches seems highly desirable in the short term for Great Lakes management.

(b) Bioenergetic models — Growth rate estimates are a cornerstone of production calculations. It follows that the principles of bioenergetics that are reflected in the regulation of growth rate are a cornerstone of measuring production processes. Models of energy budgeting based on the size and temperature dependence of feeding and metabolic rates have been developed from various perspectives (Brett and Groves 1979). They range from single-species models designed to evaluate energetic constraints on evolution of life histories (Ware 1980) to multispecies models of complex food webs that use energetics as a means for estimating predator–prey interactions (Andersen and Ursin 1977; J.E. Beyer, unpubl. data).

A singular merit of the energetics approach is that the imposition of mass balance constraints used to construct energy budgets restricts the behaviour of models within realistic biokinetic limits set by the study environment and the genetic potential of the species of interest. Thus the energetics modelling process has rules and conditions unlike those of conventional population, community, and ecosystem models which have little other than the bounds of logic and experience: energetics models (while consistent with theoretical principles) are basically empirical, and therefore provide a substantive basis for developing and testing quantitative theory. In most cases, the basic parameters defined in the elaboration of this approach derive from biological processes that can be or have been independently measured.

A primary use of energetics models in the development of management tools derives from their value in formulating and testing quantitative theory. Among the key unknowns in fisheries models is a reliable estimate for the values taken by the natural mortality rate, M, throughout the life history of a stock. A major component of M is predation on the species or life history stage of interest. Energetics models constructed for the predators of interest yield independent estimates of that proportion of M which can be ascribed to a particular predator, and an indirect means for estimating the role that management actions can play in regulating M as well as the more traditional techniques used to regulate fishing mortality, F. For example, the extensively used virtual population analysis (VPA) techniques become much more powerful if a point estimate of total mortality, Z, can be used to calibrate the calculation framework. Obviously, adequate and independent estimates of both F and M are primary requisites, and a quantitative measure of predation as a component of M is a desirable first step.

For similar reasons, bioenergetic considerations apply equally to larger-scale community models, such as those dealing with biomass spectra in integral ecological systems (Sprules and Munawar 1986). It is clear from empirical observation that the orderly, size-dependent behaviour of natural particle distributions reflects a basic constraint on the organization of biological production systems. Although a comprehensive theory to account for these observations remains to be developed, enough has been done to show that bioenergetic considerations provide the requisite basis for its formulation.

There is, for example, exemplary experimental confirmation (Werner 1984) to show that the kinds of size-dependent feeding and growth efficiency stanzas (K-lines) postulated by Paloheimo and Dickie (1966) are real and can be usefully combined with salient considerations such as predation risks that are equally amenable (Werner 1984) to quantification in bioenergetic units. Similar considerations, in combination with size-dependent constraints on metabolic rate, foraging patterns, and prey-predator relationships, appear to underlie the orderly size

structures observed at various community levels of organization within the production system.

Bioenergetic procedures, in short, offer an independent and biokinetically realistic approach to parameter estimation for other, complementary procedures used in production analysis. In addition, they provide considerable insight into the organization and function of production processes at population and community levels. In the specific context of ASPY, it is worth noting that bioenergetic procedures and parameters are particularly well-developed for many temperate freshwater species; hence, Great Lakes communities are examples of situations where further applications and development are to be encouraged.

(c) Food-web reconstruction models — Several different dynamic ecosystem models have been devised for a number of lakes (Walters et al. 1980). These models attempt to describe both the production of whole lake systems and the production of defined communities within those systems. Each past ecosystem simulation incorporates some novel aspects of production theory and its application and should be consulted when an all-encompassing ecosystem simulation is attempted for one of the Great Lakes.

Comprehensive ecosystem simulations attempt to use all available pertinent knowledge to simulate dominant ecosystem processes, as well as temporal and spatial fluctuations in those processes. These simulations have been used for assessment of marine fish resources, their natural fluctuations, and their response to the fishery in a number of oceanic and coastal regions. One simulation has been applied to a northern semiclosed fjord (Balsfjord) in order to assess current production of various ecosystem components and to evaluate various measures of enhancing local cod stocks.

Comprehensive ecosystem simulation is process oriented and time dependent. It consists of a diagnostic phase and a prognostic phase. The diagnostic phase involves an attempt to assess the abundance of various species and/or ecological groups and their production levels under a well-defined set of equilibrium conditions. The prognostic phase may involve some reconstruction of the past history of the system, but its primary purpose is the evaluation of the effects of different fishing intensities, as well as environmental anomalies, on the stocks and on the ecosystem components as a whole.

The biomass-based conditionally unstable simulation approach has been described by Laevastu and Larkins (1981). Other ecosystem models (e.g. Andersen and Ursin (1977), a conditionally stable model) are based largely on single-species models. They are number based and require stock–recruitment relationships as input. Another type of ecosystem simulation, GEMBASE (Radford and Joint 1980), requires empirically measured transfer coefficients. In the Great Lakes, several ecosystem simulation models have been developed. The Lake Ontario model by Scavia (1980) computes the pathways of carbon (including its detrital phase) and accounts for vertical heterogeneity by dividing the ecosystem into epilimnetic, hypolimnetic, and sediment subsystems. One of the principal uses of the biomass ecosystem simulation is to estimate sustainable biomass levels, by age group, for individual fish species, given estimates of plankton and benthos production as well as fish diet and food requirements. The dominant processes incorporated in the simulation include availability-dependent (or density-dependent) predation mortality, the largest component of natural mortality. This is simulated in detail as a function of both space and time. The simulation of interspecific predation enables the identification of a significant fraction of recruitment fluctuations in a quasi-realistic manner. Inclusion of the effects of environmental (e.g. temperature) anomalies permits the additional estimation of their impact on larval recruitment and on temperature-dependent growth and food requirements. Consequently the use of uncertain and variable spawning stock—recruitment estimates is unnecessary in these simulation models. Initial values for many parameters can often be obtained from the literature and refined later through simulation and observation.

Every ecosystem simulation must be verified and validated to ascertain the degree to which it reproduces the behaviour of the natural ecosystem. Ecosystem simulations are themselves complex systems consisting of a number of empirically derived formulae. These formulae are used to compute a number of dependent variables in interlocking time steps, creating a nonlinear system. The verification of the simulation is done by testing individual formulae against empirical data, checking the logical flow of the computations, and, above all, with the use of sensitivity analysis.

The value of ecosystem simulation lies in essence in the study of the behaviour of the system. In well-studied lakes (like the Great Lakes), this could be accomplished by simulating past events. Validation of prognoses depends partly on future resource surveys, but may offer prospects for particular observations of selected events within the system.

Examples of past applications of ecosystem simulation are available in the form of documented computer programs. However, these programs can, in general, be used only as guides in new applications.

(d) Production assessments based on multispecies yields — There has been much interest recently in the assessment of the recruitment and mortality rate components of net production, using yield data from several interacting species. Two basic approaches that have been developed are as follows.

(i) Multispecies virtual population analysis (MSVPA): Harvest data are combined with "catch" estimates for natural predators to back-calculate how big the stocks must have been to produce the catches. Natural predator catch rates are based on estimates of feeding rates (usually from growth plus diet composition data) and predator abundances.

(ii) Mortality rate regression analysis: Age composition data are used to estimate total mortality rates Z_t for each prey species and stock sizes (usually by VPA) for predator species. The total rates Z_t are then regressed on fishing effort and predator abundances, in a multiple regression format. The predator regression coefficients can be used to estimate food consumption rates for the predator, provided total prey abundance can also be estimated.

These approaches are complementary: MSVPA uses data on predator abundance and growth to estimate prey abundance, while the regression methods provide a direct measure of the effect of predator abundance on prey mortality rate.

An elegant compression of the MSVPA methods has been developed by T. Laevastu and N. Bax (unpubl. data) with their "top-down" equilibrium calculations of the lower trophic level abundances that must be present to sustain the estimated levels of production/consumption at the higher trophic levels. These calculations require comprehensive data on all major species in the ecosystem.

Total yield and age/size composition data are essential to these approaches, along with size/age-specific information on

growth, feeding rates (or growth efficiency), and diet composition. Such data are available for a variety of species in the Great Lakes, particularly the salmonids and their main forage species. These approaches may provide valuable insights into the forage fish "crisis" that is now a concern in the Great Lakes.

(e) Cohort analyses — Principal methods employed here are the "Allen curves," fully described in Edmondson and Winberg (1971), and the VPA methods which are covered in detail elsewhere in ASPY. We do not deal further with them here.

Relations of Production to Community Development

A body of thought developed in terrestrial ecology distinguishes between immature and mature systems as characteristically supporting different levels of productivity. These ideas have been applied in plankton ecology to justify classifying natural communities into two broad categories: diverse, loosely connected systems which exhibit both high variability and high productivity and sparse, tightly connected systems which exhibit both low variability and low productivity. These classifications are consistent with the view that there is a trade-off between general levels of productivity and control. They would also lead to the expectation that more productive systems will inevitably be characterized by greater variability. While it is true that harvesting of populations of fish inevitably results in a lowered average age towards some "critical" age or size at which surplus production is maximized, and that the same argument applies within a given multispecies complex, it is not certain that the same ideas can be applied to the successional sequences of species groups noted in the Great Lakes. Nor is it clear how any such relationships would be altered by such factors as introductions, deforestation, and eutrophication, all of which have had some influence on these lakes.

In the same context, it is clear from a number of papers at this symposium that predator–prey linkages must be as responsible for variability at the upper trophic levels as are variations in the input nutrients and primary production at lower trophic levels (see especially McQueen et al. 1986; but also Stewart et al. 1981; Kitchell and Hewett 1987). Crowder et al. (1987), among others, speculated that changes in zooplankton structure may also result from predation. The phenomenon of predator control of consumer species is well-established and is clearly important enough to be considered explicitly in investigations of the functional linkages among community structure, stability, and levels of productivity in Great Lakes systems. A better knowledge of these relationships appears to be vital to an understanding of the relative merits of lake rehabilitation programs.

Potential Fish Production and Yield of the Great Lakes and Lake Winnipeg

Constraints of time and data availability naturally limit the practical application of all of the foregoing methodologies in predicting potential fish production and yield. We have selected three approaches which we believe can be readily applied to existing Great Lakes data bases. Although the approaches vary considerably in complexity, all have the potential to be useful management tools. Their precision and reliability will be improved as the requisite data bases are refined and enhanced.

Potential Fish Yield from Empirically Derived Estimators

We selected eight empirical models which had been derived from limnological variables. Since the models use yield statistics as the dependent variable, they predict potential fish yield as an indication of potential production. The relationship between fish yield and fish production has not been clearly defined in these situations. Ryder (1965) regarded yield as a reliable estimate of fish production, and in a later discussion (Ryder et al. 1974) concluded that long-term averaging of yields from a moderate-to-intensive-effort fishery will result in estimates approaching the maximum equilibrium yield. Extensive IBP studies (Morgan 1980) suggest that total production of fish in an ecosystem is roughly twice that of the adult population biomass and may be as much as 10 times the yield of edible fish.

Data used in the eight models are given in Table 2 and the derived yield estimates are summarized in Table 3. The empirically derived estimates are compared with Matuszek's (1978) estimate of maximum sustained yield (MSY) for the Great Lakes and Lysack's (1986) yield estimate for Lake Winnipeg. Matuszek (1978) used a 15-yr period of maximum commercial catch plus estimates of sport and mink ranch harvest as a basis for estimating MSY. Historic harvest data, if selected carefully, are useful estimators of potential yields and are used in this paper to compare the performance of empirically derived and other predictors.

Given that the various indices are used to predict fish yield, there is reason to expect some convergence of the estimates, and indeed, the range of predictions is reasonably narrow. The best overall empirically derived estimator of fish yield in the Great Lakes is the MEI, especially for the upper Great Lakes where it predicted yields within 19% of Matuszek's MSY. The MEI estimate is low for Lake Erie where cultural eutrophication has increased productivity beyond that expected from the index. Oglesby (1977) considered that culturally influenced lakes can produce considerable deviations in production from estimates given by the MEI. Standardizing the mean depth at 25 m, as suggested by Oglesby (1977), did not improve the MEI estimates for the Great Lakes. The MEI estimate for fish yield from Lake Ontario is considerably more than Matuszek's MSY. Mean depth and TDS (and therefore the MEI) in Lake Ontario and Lake Michigan are roughly similar which would lead us to expect that fish yield should be comparable. Transfer efficiency calculations (output of fish in relation to primary production on a carbon basis) indicate that Lake Ontario is an extremely inefficient system in relation to the other Great Lakes (Sprules and Munawar 1986) and, on a global scale, to the IBP lakes (Morgan 1980). The MEI yield probably approximates what the Lake Ontario system should be producing. The low yield has been attributed to disruption of vertical vectoring of energy caused by the recent loss of major fish species (Christie et al. 1987).

The total phosphorus (TP) equation of Hanson and Leggett (1982) underestimates fish yield in most of the Great Lakes although for 21 north-temperate lakes it was a better predictor of yield than TDS, mean depth, surface area, and the MEI. The shortcomings of TP as a yield estimator in the Great Lakes may be due to several factors, including insufficient and unreliable phosphorus data, particularly in the upper Great Lakes, and variability in the response of phytoplankton to TP concentrations. Sources of variability in phosphorus and chlorophyll data have been discussed recently by Knowlton et al. (1984).

Yield estimates from Oglesby's (1977) equation using phytoplankton productivity are variable with best predictions for Lakes Superior, Michigan, and Erie. Data on primary productivity in the Great Lakes are scarce, measurements have

TABLE 2. Limnological variables for the Great Lakes and Lake Winnipeg.

Lake	Area (km^2)[a]	$\bar{z}$ (m)[a]	TDS ($mg \cdot L^{-1}$)[a]	Total P ($mg \cdot m^{-3}$)[b]	Temp. (°C)[c]	Chl *a* ($mg \cdot m^{-3}$)[d]	PP ($g\,C \cdot m^{-2} \cdot yr^{-1}$)[d]	Macrobenthos ($kg \cdot ha^{-1}$) (dry weight)[g]
Superior	82 414	148.0	60	3.3	3.9	1.0[e]	90	0.9
Michigan	58 016	84.0	134	6.6	7.7	2.1[f]	145	34
Huron (main lake)	41 659	61.0	108	4.4	6.6	1.0	90	14.8
Erie	25 690	18.5	146	17.8	9.4	5.0	245	46.3
Ontario	19 477	80.5	148	19.4	8.1	3.8	185	18.4
Winnipeg	23 750[h]	12.0[h]				2.3[i]		8.0[h]

[a]Matuszek (1978).
[b]Dobson et al. (1974).
[c]Schlesinger and Regier (1982).
[d]Oglesby (1977).
[e]Munawar and Munawar (1978).
[f]Vollenweider et al. (1974).
[g]Alley and Powers (1970).
[h]Lysack (1986).
[i]G. J. Brunskill (pers. comm.).

TABLE 3. Summary of yield statistics and potential yield estimates from eight empirical models for the Great Lakes and Lake Winnipeg. Y_1 = yield ($kg \cdot ha^{-1} \cdot yr^{-1}$); Y_2 = yield ($g\,C \cdot m^{-2} \cdot yr^{-1}$); Y_3 = yield ($g \cdot m^{-2} \cdot yr^{-1}$ (dry weight)); Y_4 = yield (kg); ME1 = $TDS/\bar{z}$ ($mg \cdot L^{-1}/m$); TP = total phosphorus ($mg \cdot m^{-3}$); PP = phytoplankton production ($g\,C \cdot m^{-2} \cdot y^{-1}$); Chl $a = \bar{x}$ summer chlorophyll *a* ($mg \cdot m^{-3}$); $T = \bar{x}$ annual air temperature (°C); A_0 = lake area (km^2); B = macrobenthos ($kg \cdot ha^{-1}$) (dry weight).

Lake	Yield ($kg \cdot ha^{-1} \cdot yr^{-1}$)[a]	Potential fish yield ($kg \cdot ha^{-1} \cdot yr^{-1}$)							
		ME1[b]	TP[c]	PP[d]	Chl *a* 1[e]	Chl *a* 2[f]	T[g]	A_0[h]	Benthos[i]
Superior	1.19	0.98	0.24	0.81	0.48	0.30	1.91	1.62	0.75
Michigan	2.24	1.82	0.49	2.10	1.14	1.79	3.26	1.72	7.23
Huron	2.09	1.92	0.32	0.72	0.48	0.30	2.79	1.82	4.3
Erie	9.72	3.70	1.34	6.0	3.16	5.70	4.13	1.97	8.77
Ontario	1.25	1.91	1.46	3.42	2.29	4.08	3.44	2.07	4.93
Winnipeg	2.57[j]				1.27	2.06		2.0	2.93

[a]Matuszek (1978).
[b]Ryder (1965): $\log Y_1 = 0.168 + 0.446 \log ME1$.
[c]Hanson and Leggett (1982): $\log Y_2 = -1.148 + 1.021 \log TP$.
[d]Oglesby (1977): $\log Y_2 = -6.00 + 2.00 \log PP$.
[e]Oglesby (1977): $\log Y_3 = -1.92 + 1.17 \log Chl\ a$.
[f]Oglesby et al. (1987): $Y_1 = -1.047 + 1.349\ Chl\ a$.
[g]Schlesinger and Regier (1982): $\log Y_1 = 0.043 + 0.061T$.
[h]Youngs and Heimbuch (1962): $\log_e Y_4 = 7.01 + 0.83 \log_e A_0$.
[i]Matuszek (1978): $\log Y_1 = -0.098 + 0.625 \log B$.
[j]Lysack (1986).

not been uniform spatially, temporally, or in terms of methodology, and consequently average annual estimates are little more than "best estimates" (Vollenweider et al. 1974). The potential of this estimator in tropical and temperate lakes and ponds has been demonstrated by Melack (1976), Oglesby (1977), McConnell et al. (1977), Liang et al. (1981), and others. Its practical application to the Great Lakes must await the collection of additonal data which are difficult and expensive to obtain.

Yield estimates from standing crop of phytoplankton, expressed as chlorophyll *a*, are less difficult and cheaper to obtain. In Table 3, estimates of yield predicted from Chl *a* 1 are based on a log-transformed regression (Oglesby 1977) whereas the data used in the Chl *a* 2 estimate were not transformed (Oglesby et al. 1987). Both regressions predicted fish yields below Matuszek's MSY (except for lake Ontario) with the arithmetic model producing more variable estimates. The Great Lakes chlorophyll *a* data are themselves variable due to temporal and spatial differences in measurement. In addition, there are physiological and ecological considerations associated with using chlorophyll *a* as an indicator of algal biomass (Nicholls and Dillon 1978). Although chlorophyll *a* has the potential to be a practical estimator of fish yield (Oglesby 1977), more data collection and model refinement are required for its useful application to the Great Lakes.

The mean annual temperature model of Schlesinger and Regier (1982) overestimated the MSY for all lakes except Lake Erie. Since the regression equation represents the relationship between temperature and MSY for 43 lakes from a span of 77° latitude, it should not be expected to accurately predict yields on a regional basis. Other studies (Matuszek 1978; Schlesinger and

McCombie 1983) have shown that climate over a narrow latitude range is not a good predictor of yield from commercial and sport fisheries.

Reasonable estimates of yield for Lakes Michigan, Huron, and Winnipeg were obtained from the surface area model of Youngs and Heimbuch (1982). Lake Superior and Lake Ontario yields are overestimated probably because of the large deep areas of unproductive water in those lakes. On the other hand, Lake Erie is an obvious outlier because its productivity is more significantly related to nutrients and shallow depth than surface area.

The macrobenthos model of Matuszek (1978) appears to be a good predictor of fish yield in Lake Erie and Lake Winnipeg and a fair predictor for lake Superior. The prediction for Lake Michigan is relatively large which may be a reflection of the inadequacy of the data. Matuszek (1978) and Hanson and Leggett (1982) have shown the strength of macrobenthos biomass as a predictor of potential fish yield. Clearly, there is a need for improved estimates of benthic biomass and production in the Great Lakes.

Several of the empirical models were found to be unsatisfactory for yield estimation in Lake Winnipeg. This was due to effects of the large watershed and shallow lake basin on turbidity and nutrient and TDS loadings, which are high, and water residence times, which are short (Lysack 1986).

As emphasized by most of those who developed the equations used in Table 3, precision is dependent on similarity between the lake for which prediction is sought and those used in deriving the relationship (Jones and Hoyer (1982) have described a good example). Because of their scale, the Great Lakes do not always fit the norm for north-temperate lakes and therefore, it is surprising that the various limnological indicators have produced such a narrow range of predictions of potential fish yield.

Potential Fish Production Estimated from Invertebrate Production (Borgmann Model)

Recent advances in the modelling of biomass and energy flow up pelagic food webs (e.g. Sheldon et al. 1977; Platt and Denman 1977, 1978; Silvert and Platt 1980; Borgmann 1982, 1983) provide a clearer understanding of the relationship between fish biomass and production and production at lower trophic levels. Sheldon et al. (1977) and Borgmann et al. (1984) have used such models to predict potential fish production in the sea and Lake Ontario, respectively. The same approach is used here to predict fish production in each of the Great Lakes and Lake Winnipeg from estimates of zooplankton and benthic invertebrate production. Invertebrate production has not, however, been calculated directly for all species, and total production must therefore be inferred from a combination of biomass and turnover rate data as demonstrated below.

1. Zooplankton production

Zooplankton biomass in different zones of Lake Superior ranges from 6.4 to 24.6 $mg \cdot m^{-3}$ dry weight for the upper 100 m. In the offshore waters east of Isle Royale and the Keweenaw Peninsula, which comprises the largest zone, biomass was estimated at 11 $mg \cdot m^{-3}$. Offshore waters west of this zone contained 7 $mg \cdot m^{-3}$ (Watson and Wilson 1978). Lake Superior zooplankton biomass is therefore roughly 10 $mg \cdot m^{-3}$, or about 1 $g \cdot m^{-2}$. Zooplankton biomass in Lakes Huron, Erie, and Ontario are given in Watson and Carpenter (1974, table 4). The annual averages are summarized in Table 4. For these three lakes, net hauls were made over the top 50 m or from 2 m off the bottom, whichever was less. Total biomass per unit area for Lakes Huron and Ontario was estimated by multiplying the numbers in Table 4 by 50 m. For Lake Erie, which is much shallower than the other lakes, biomass per unit area was estimated from volume biomass × 18.5 m, the average depth of the lake. Lake Michigan zooplankton biomass is approximately 60 $mg \cdot m^{-3}$ over the top 50 m, giving a total biomass of about 3.0 $g \cdot m^{-2}$ (Hawkins and Evans 1979). Lake Winnipeg zooplankton biomass (15 $g \cdot m^{-2}$ wet weight: area weighted mean from data in Lysack 1986) was estimated from wet weight assuming a moisture content of 90%.

Borgmann et al. (1984) obtained an overall production to biomass ratio of 18 for the epilimnetic crustacean plankton of Lake Ontario in 1981. Zooplankton production per unit area of all the Great Lakes was estimted as 18 × biomass per square metre of lake surface (Table 4). Turnover rates for the total zooplankton community, including the deeper zooplankton, are probably lower, except perhaps in Lake Erie. However, in the absence of specific zooplankton production estimates for most of the lakes, 18 $\cdot yr^{-1}$ will have to suffice as a rough approximation.

2. Benthic production

Benthic biomass for the Great Lakes was given by Alley and Powers (1970). Biomass for Lake Winnipeg was estimated from the wet weight data given by Lysack (1986, data from M.Sc. thesis of Flannigan (1980); O.A. Saether, unpubl. data) assuming a moisture content of 90%. Benthic production has been estimated for Lakes Ontario (Cook and Johnson 1974) and Winnipeg (Lysack 1986), giving turnover rates of 1.36 and 5.1 $\cdot yr^{-1}$ for these lakes, respectively. Benthic turnover rates are therefore much higher in shallow Lake Winnipeg as compared with the much deeper Lake Ontario. Johnson and Brinkhurst (1971) observed a similar drop in benthic turnover rates in the Bay of Quinte with increasing depth. It is therefore not possible to use a constant turnover rate to estimate benthic production from biomass. As an initial approximation, we can assume an allometric relationship between lake depth and benthic turnover (P/B) rates, fitted to the data for Lakes Winnipeg and Ontario, giving $P/B = 28.6 \times (\text{mean depth})^{-0.694}$. This provides P/B estimates of 3.78, 1.65, 1.32, and 0.89 for Lakes Erie, Michigan, Huron, and Superior, respectively, and gives the production estimates shown in Table 4.

3. Mysid production

Mysids (*Mysis relicta*) in the Great Lakes are both planktonic and benthic, depending on time of day and water depth. Their production is not included in the above estimates and is summarized here.

Mysid production in Lakes Ontario and Superior was estimated by Borgmann (1983) and by Sell (1982) for Lakes Michigan and Huron. Borgmann's estimates for Lake Ontario are lower than those made by Sell for Lake Huron, even though turnover rates were similar and both authors used data from Capenter et al. (1974) which indicated higher mysid biomass in Lake Ontario. This is because Sell estimated production only over the deeper stations whereas Borgmann estimated production averaged over the entire lake (including the shallow areas containing no mysids). The calculations of Sell, therefore, provide an overestimate of the lakewide average mysid production for Lake Huron. Using data from four sources, Sell (1982) obtained production estimates for Lake Michigan ranging from 0.25 to 3.2 $g \cdot m^{-2} \cdot yr^{-1}$. Again, the highest value is probably an overestimate for the lakewide mean mysid production.

TABLE 4. Potential fish production in the Laurentian Great Lakes and Lake Winnipeg predicted from invertebrate production. Production is estimated for either large (1000 g) or small (50 g) fish. Also shown is estimated total production for all fish greater than 17 g. All weight units are dry weight except the conversions to $kg \cdot ha^{-1}$ which are wet weight.

	Superior	Michigan	Huron	Erie	Ontario	Winnipeg
Mean depth (m)	148	84	61	18.5	80.5	12
Zooplankton biomass ($mg \cdot m^{-3}$)	10(100)[a]	60(50)[b]	51(50)[c]	188(18.5)[c]	48(50)[c]	125(12)[d]
Zooplankton production ($g \cdot m^{-2} \cdot yr^{-1}$)[e]	18	54	46	63	43	27
Benthos biomass ($g \cdot m^{-2}$)	0.09[f]	3.4[f]	1.48[h]	4.63[f]	1.84[f]	0.81[g]
Benthos production ($g \cdot m^{-2} \cdot yr^{-1}$)[i]	0.08	4.5	2.4	17	2.5[h]	4.1[g]
Mysid production ($g \cdot m^{-2} \cdot yr^{-1}$)	0.26[j]	<3[k]	<1.5[k]	0	0.64[j]	0
Total production	18	58–62	48–50	80	46	31
d (equation 1)	−0.29	−0.96	−0.78	−1.27	−0.73	−0.49
F_s (equation 3)	0.60	2.0	1.6	2.7	1.5	1.0
P(1000-g fish)						
$g \cdot m^{-2} \cdot yr^{-1}$	0.10	0.33	0.27	0.44	0.25	0.17
$kg \cdot ha^{-1} \cdot yr^{-1}$	4.0	13.2	10.8	17.6	10.0	6.8
P(50-g fish)						
$g \cdot m^{-2} \cdot yr^{-1}$	0.22	0.72	0.59	0.96	0.55	0.37
$kg \cdot ha^{-1} \cdot yr^{-1}$	8.8	28.8	23.6	38.4	22.0	14.8
P(>17-g fish)						
$g \cdot m^{-2} \cdot yr^{-1}$	0.14	0.46	0.37	0.61	0.35	0.24
$kg \cdot ha^{-1} \cdot yr^{-1}$	5.6	18.4	14.8	24.4	14.0	9.6

[a]Watson and Wilson (1978); numbers in parentheses are sampling depths.
[b]Hawkins and Evans (1979).
[c]Watson and Carpenter (1974).
[d]Lysack (1986) from unpublished data of Patalas, and assuming 90% moisture content.
[e]Assuming turnover rate of $18 \cdot yr^{-1}$.
[f]Alley and Powers (1970).
[g]Lysack (1986) from Flannigan (M.Sc. thesis), and assuming 90% moisture content.
[h]Cook and Johnson (1974).
[i]Biomass × 28.6 × (mean depth)$^{-0.694}$.
[j]Borgmann (1983).
[k]Sell (1982); but not averaged lakewide.

4. Potential fish production

Potential fish production can now be estimted from invertebrate production using the following relationships:

(1) $P_{xy} = d(W_y^{-\epsilon} - W_x^{-\epsilon})$

(2) $P = F_s W^{-\epsilon}$

(3) $F_s = -\epsilon d \ln (\text{PPR})$

where P_{xy} in equation 1 represents total production between body sizes W_x and W_y and ϵ is particle-size-conversion efficiency and d is a constant (equation 6 in Borgmann 1987). Equation 2 is another way of defining production, but in this case, P represents production at a point body size W and F_s is a constant (a measure of biomass flow up the size spectrum). In a food web, P represents production of all organisms at size W, plus the flow of biomass from organisms below size W which are eaten by those above size W. This is equivalent to what would be the production of a hypothetical species with all individuals having body size W if all production at smaller sizes were consumed by this species before being available to larger sized organisms (e.g. Borgmann 1983). Equation 1 is applicable when data are available on total production over a size interval (as in the case of our invertebrate production estimates) whereas equation 2 is utilized if biomass flow past a given size is to be estimated. Equation 3 gives the relationship between the constants d and F_s in equations 1 and 2 where PPR is the mean predator–prey size ratio (table 1 in Borgmann 1987).

Another way of expressing potential production, which is sometimes useful when dealing with commercial yields, is as production of all organisms above a certain size W_0. This can be done by setting $W_x = W_0$ and W_y = infinity, giving

(4) $P_{>W_0} = -d \cdot W_0^{-\epsilon} = F_s W_0^{-\epsilon} / (\epsilon \ln (\text{PPR}))$.

This modified form of equation 1 may be applicable when comparing predicted production with commercial yields of fish where all above a minimum size are harvested.

It is worth emphasizing that calculations employing equation 1 are based on size classes and not on trophic levels. This is why it is possible to add, for example, mysid production to zooplankton production in equation 1, even though mysids feed to some degree on zooplankton and therefore represent a higher trophic level. Size spectrum analyses of this type avoid the need to specifically identify trophic levels.

The next step in estimating potential fish production is to specify the width of the invertebrate size class. Borgmann (1985) assumed a size range from 10^{-7} to 10^{-5} g dry weight for the epilimnetic zooplankton. This does not include the larger species such as *Diaptomus sicilis* and *Limnocalanus macrurus*. *Limnocalanus macrurus* adults reach a size of about 47 μg (Wilson and Roff 1973). The size range of the crustacean zooplankton therefore is about 0.1–50 μg dry weight. Mysids range in size from roughly 50 μg to 10 mg dry weight, and *Pontoporeia affinis*, the largest benthic invertebrate, is of similar size. This gives a total size range for the invertebrates of 10^{-7} to 10^{-2} g dry weight (W_x and W_y in equation 1).

We can now estimate d in equation 1 if we use the value of ϵ estimated for Lake Ontario (0.26) by Borgmann and Whittle (1983). Rearranging equation 1 and using P_{xy} equal to the invertebrate production values listed in Table 4 gives estimates of d for each of the lakes (Table 4). F_s can then be calculated from equation 3 using an average predator–prey size ratio of about 3000 on a weight basis (e.g. Sheldon et al. 1977; Peterson and Wroblewski 1984). This then allows prediction of potential fish production for any size of fish using equation 2. Table 4 gives examples for fish sizes of 1000 g (about 4000 g wet weight) and 50 g (about 200 g wet weight). The first represents production which could support a fishery for large fish only whereas the second is production which could support a fishery based on smaller sized fish alone. If more than one size is harvested, then fish production would be intermediate (see Borgmann et al. (1984) for a sample calculation).

In practice, fish are caught over a wide range of sizes above some minimum size. Since fish include the top predators in the Great Lakes, a useful estimate of total potential fish production could be made using equation 4 and setting W_0 equal to the lower size limit of harvested fish (about 17 g, see below). Estimates of total fish production, described in this way, are also listed in Table 4. This estimate of fish production is intermediate between the estimate of production past a point size for large and small fish (i.e. at 1000 and 50 g). It is larger than the estimate for large fish production because it includes the production of smaller fish. It is smaller than the estimate for production past a point size of 50 g because production past a point size of 50 g with a mean PPR of 3000 is analogous to production over a size range of roughly 1.8–5400 g (i.e. one trophic level), which includes production by still smaller fish.

The estimate of F_s in Table 4 for Lake Ontario is larger than the value obtained by Borgmann et al. (1984). This is primarily because the zooplankton biomass is based on the data of Watson and Carpenter (1974), which included all zooplankton within the top 50 m, and is larger than the epilimnetic zooplankton biomass estimates in Borgmann et al. (1984). The zooplankton data of Watson and Carpenter are used in Table 4 because equivalent data are available for the other lakes. It is possible, however, that the resultant estimate of F_s is too high because the turnover rates for the total zooplankton population may not be as high as the $18 \cdot yr^{-1}$ predicted for the epilimnetic zooplankton (Borgmann et al. 1984). This serves to emphasize that the potential fish production estimates summarized in Table 4 are crude, first-order approximations. These should be improved by obtaining direct estimates of zooplankton and benthic production for all major species in the 10^{-7} to 10^{-2} g size range in all of the lakes. Furthermore, separate estimates of ϵ for each of the lakes should be made. It must also be remembered when interpreting these calculations that "potential" means estimated, assuming all prey organisms are consumed by some predator. Actual production will therefore be somewhat less.

Potential Fish Production and Yield Estimated from the Borgmann Model with Population Parameter Modifications (Shuter Method)

The commonly harvested fish species of the Great Lakes can be separated into two broad groups: "small" fish (i.e. perch, lake herring, bloater, alewife, smelt) and "large" fish (i.e. walleye and its near relatives, lake trout, whitefish). In this section, we show that these two groups are characterized by quite different life history parameters. We then illustrate how lake-specific potential yield for each group can be estimated by combining these parameters with the Borgmann (1987) production model, empirical information on population P/B ratios (Banse and Mosher 1980; Dickie et al. 1987), and classical population dynamics theory (Deriso 1987). Finally, we compare these estimates of potential yield with historical sustained yields observed in each of the lakes.

A review of the literature on the species listed above demonstrated (Table 5) that the small species had relatively similar values for the following life history parameters: von Bertalanffy growth coefficient (K), asymptotic length (L_∞) and weight (W_∞), and weight at first maturity (W_{mat}). The large species also had similar values for these parameters but they differed markedly from the values for small species. Given these results, we decided to characterize each size group by a single set of average parameter values assumed to be common across the Great Lakes.

Lake-specific values (Table 5) for the instantaneous natural mortality rate (M) for each size group were estimated using Pauly's (1984) empirical relationship:

$$\log_{10} M = -0.006 - 0.279 \log_{10} L_\infty + 0.6543 \log_{10} K + 0.463 \log_{10} \bar{T}$$

where $\bar{T}$ is the average annual water temperature (degrees Celsius) for the lake. Estimates of $\bar{T}$ for each lake were obtained using methods outlined in Shuter et al. (1983).

Historically, commercial fishing on the Great Lakes has been directed against organisms which exceed 15–20 cm in length, corresponding to about 17 gm dry weight. The total potential production that can be expected from all organisms that exceed a specific size (W_0) can be calculated for each lake using equation 4 (previous section). The following assumptions underlie such calculations: (i) there is no upper bound on the size range of organisms that exceed W_0; (ii) both the PPR and the particle-size-conversion efficiency (ϵ) are constant for all organisms which exceed W_0 and do not vary from lake to lake. The data in Table 5 demonstrate that there is an upper bound on the size range; however, our analyses of the growth data on large fish suggested that the value of PPR decreases when these animals reach a size similar to the L_∞ for small fish. Walford plots of growth data from Great Lakes populations of large species

TABLE 5. Life history parameters for different size groups of fish. Parameter estimates were obtained from data on Great Lakes populations of perch, lake herring, bloater, and smelt (small fish) and lake trout, lake whitefish, walleye, and blue pike (large fish) obtained from Scott and Crossman (1973), Carlander (1969, 1977), and Parsons (1967). Lake-specific values for M were obtained using Pauly's (1984) regression equation.

	Small fish		Large fish	
Parameter	Representative value	Range	Representative value	Range
K	0.31	0.16–0.51	0.20	0.18–0.25
L_{00}(mm)	315	260–350	750	700–850
W_{mat}(g dry weight)	25	12–43	112	100–125
W_{00}(g dry weight)	100	60–120	1125	950–1625
M				
Superior	0.23		0.13	
Huron	0.26		0.15	
Michigan	0.27		0.16	
Erie	0.30		0.18	
Ontario	0.28		0.16	

consistently exhibited a pattern consisting of two phases. In early life, growth was similar to that exhibited by small fish; on reaching a length of about 300–400 mm, a new growth curve emerged with a much higher L_∞. Since the separate effects of a decreasing PPR and an upper size limit would tend to cancel each other out, we reason that the equation given above can be used to obtain a first-order estimate of the total production from all fish exceeding the minimum harvestable size.

The minimum harvestable size for small fish (17 g dry weight) is quite similar to the value of W_{mat} for small fish. This is consistent with Pauly's (1984) contention that directed exploitation on a stock generally begins when fish reach a size similar to W_{mat}. Since W_{mat} for large fish (112 g dry weight) is relatively similar to W_∞ for small fish (100 g dry weight), we felt that it was possible to describe the situation by assuming that the total production of harvestable fish could be subdivided into two categories: production generated by fish in the size range 17–112 g (corresponding to harvestable small fish) and production generated by fish in the size range 112–1125 g (corresponding to harvestable large fish).

In order to split our estimate of total production into estimates of potential production for each size group, we made use of the following assumptions: (i) the biomass spectrum for fish is essentially flat; since small and large size intervals are roughly equal, on a log scale, the standing biomass for small fish is similar to that for large fish: this is a common assumption in size spectrum models (e.g. Borgmann 1985; Sheldon et al. 1977) and has some empirical support, at least for lower trophic levels (e.g. Sprules and Munawar 1986); (ii) within the fish community, P/B is allometrically related to body weight with a slope of approximately -0.4 (Banse and Mosher 1980; Dickie et al. 1987): this steep negative slope reflects the fine-scale structure of the size spectrum within natural populations of fish; the coarse structure of the spectrum is reflected in the shallower slope (approximately -0.26) generally obtained when organisms ranging from unicells to vertebrates are compared (Banse and Mosher 1980); (iii) the average P/B ratio within each size group of fish can be represented by the P/B ratio for individuals with a size equal to the geometric mean of the bounds for the group size interval: mean size small group = 46 g dry weight; large group = 355 g dry weight. Assumptions (i) and (ii) permit the conclusion that, within the fish, total production is allometrically related to individual weight with a slope of -0.4. Assumption (iii) permits estimation of the percentage of total production generated by each size group: large = $(355)^{-0.4} / (355^{-0.4} + 46^{-0.4}) = 31\%$; small = 69%. Potential production for each size group was then estimated by applying these percentages to our estimate of total fish production (Table 6).

Optimum sustained yield (Y) for each size group was calculated as follows:

(i) lake and size specific values for the $F_{0.1}$ fishing mortality rates (Deriso 1987) were estimated from M and K values (Table 5) using the method given by Deriso (1987);

(ii) optimum sustained yield (Table 6) was calculated from potential production using the formula

$$Y = \frac{F_{0.1}}{F_{0.1} + M} P = \phi P.$$

Estimates of ϕ for small and large fish were essentially identical across lakes, having values equal to 0.56 and 0.57, respectively.

In order to compare potential yields with observed sustained yields, the commercial harvest data for each of the Great Lakes were examined as follows: (i) the total yield for each size group was determined by summing the yields for the member species; (ii) for each group, plots of annual yield over time were examined; extended (10–15 yr) periods which failed to exhibit a noticeable temporal trend were identified and the period which exhibited the highest average yield was selected; (iii) the average yield over the selected period was taken to represent the highest sustained yield hitherto taken from the size group. Our yield data for large fish are almost identical to Matuszek's (1978) TWWS category of taxa which included yields of lake trout, lake whitefish, walleye, and sauger. Our time intervals

TABLE 6. Lake-specific estimates of potential production and yield for harvestable fish by size category. All units are ($kg \cdot ha^{-1}$) wet weight (to convert to $g \cdot m^{-2}$ dry weight, divide by 40). The time interval used for calculating observed yields is also given.

Lake	Potential fish production	Estimated optimum yield	Observed sustained yield		Observed/ optimum (%)	MEI yield estimate
			Maximum	Interval		
Superior						
Small	3.88	2.20	0.80	1940–54	36	
Large	1.72	0.96	0.32	1940–54	33	0.98
Michigan						
Small	12.8	7.20	3.36	1966–77	47	
Large	5.6	3.20	0.68	1910–25	21	1.82
Huron						
Small	10.4	6.00	0.48	1925–38	8	
Large	4.4	2.52	0.80	1925–38	32	1.92
Erie						
Small	16.4	9.20	6.80	1958–72	74	
Large	7.6	4.40	4.40	1943–56	100	3.70
Ontario						
Small	9.6	5.60	0.32	1915–30	6	
Large	4.4	2.40	0.64	1915–30	27	1.91

are later than Matuszek's periods and therefore include data on alewife harvests which are not included in his estimates of MSY. Estimates of potential production and maximum observed sustained yield are summarized in Table 6. MEI estimates of potential yield are also included for comparative purposes.

Discussion

It was pointed out in the introduction that there is a need for simple and cheap models for fishery assessment, but that such desirable characteristics may be realized at the expense of accuracy and reliability. Several of the above models meet the criterion of simplicity, and even in the more complex calculations, many of the data utilized were collected for other purposes so that incremental costs have also been low. The accuracy and reliability of the results need to be examined carefully. Judgement depends on their apparent internal consistency, the quality of the input data, and the applicability of the models themselves.

One of the primary criteria of potential usefulness of the models arises from the consistency of the results when compared between various lakes and within the historic series of yields. For example, it has been noted in past studies that yields from Lake Ontario seem generally low compared with various measures of potential productivity. In addition, significant temporal changes in productivity patterns have been observed in several of the lakes. This raises the possibility that features which we have not taken into account may be affecting the overall efficiency of production processes. This possibility has been raised by Sprules and Munawar (1986), who showed that a fully developed biomass spectrum may provide a number of comparative features of heuristic value. Representative spectra are not yet available for all the Great Lakes, even though it now appears that this system of characterization may be one of the cheaper and quicker, as well as one of the most powerful, available. More accurate and fine-scale empirical spectra are also essential for testing the applicability of theoretical refinements such as those used in Shuter's method (see previous section) of estimating production for small and large fish.

In the absence of extensive size spectrum data, we have made use of Borgmann's approach to estimating fish production from zooplankton production. In examining the results, it was noted that the lower internal consistency may well reflect the need for refinements of input data. It must be recognized, however, that at this stage in the development of our "art," we are unable to distinguish among inaccuracies arising from errors in parameter estimation, inadequate sampling, or model oversimplification. Refinement in the quality of the data may, in fact, be an essential step in better judging the applicability of the models themselves.

Comparative ecology is a potentially powerful source of information for interpreting production and yield data. Thus it is that the low Lake Ontario yields alert us to the need for a more detailed understanding of that system. The apparently peculiar nature of Lake Ontario has a particular influence on the foregoing results of Borgmann's model, since estimates of particle-size-conversion efficiency used in it and applied to all lakes were actually derived from Lake Ontario. Clearly, this needs to be checked. Similarly, the high relative productivity and yield of Lake Erie seems to reflect its special morphology as much as it does the intense fishery. Further development of the analytic models studied in a preliminary way in this report may help to point the way to other such features.

One outstanding feature of the comparative ecology of aquatic production which seems too little examined is the remarkably low fish yield of these Great Lakes systems when compared with coastal marine systems at a similar latitude. Yield per unit surface area of the Great Lakes seems to be about an order of magnitude less than it is in comparable areas of the great marine fisheries off the east coast of Canada or in the North Sea (Dickie 1972). Since Sprules and and Munawar's (1986) comparisons of biomass spectra suggest that the efficiency of trophic transfers between freshwater and marine systems may not be remarkably different, such yield contrasts would appear to be a

function of differences in nutrient supplies and recycling between the freshwater and marine areas. It is possible, of course, that production in these inland seas should be compared with that of the open ocean, rather than the rich coastal shelves. However, the point we wish to make is that the potential power of such comparative studies is only now becoming realizable with the advent of such relationships as the biomass spectrum.

While the very format of the ASPY review process confines attention to the simpler methods, we do not wish to imply that such approaches are uniquely useful. What we have to point out is that using the simpler and cheaper approaches has resulted in a consistency of results which suggests a higher reliability than we had any a priori reason to expect. We have little experience with these methods because they are relatively new. The results encourage us to recommend that they be seriously considered as a regular part of the normal suite of investigations. The results, taken as a whole, point to the likelihood that total yields of large fish from the lakes are at about their maximum. These conclusions are in keeping with those from the quite different methods utilized by Kitchell and Hewett (1987) who found that alterations in the structure of yields in Lake Michigan are not likely to open new productive routes but will only rechannel energy and materials within the known system. It should be clear, however, that for appreciation of such complex situations, which demand information on the fine-tuning of production systems, there is no visible substitute for the more complex but better substantiated bioenergetic, food-web reconstruction described above but not yet fully applied to analysis of the Great Lakes situations.

Although we have pointed out difficulties in defining the relationship between fish yield and fish production, we used population dynamics theory to estimate optimum yields of small and large fish as constant percentages of potential production. There is evidence (Christie 1974; Ryder et al. 1974), however, that yield is not always a constant proportion of production across size classes. Therefore, our estimates of optimum yields of small fish, particularly for Lake Ontario and the upper Great Lakes, may not be actually realized. The reasons for the divergence between yield and production are unclear, but it may be partly attributable to lack of marketability of smaller species or inability or reluctance of fishermen to fish down the trophic scale due to economic or mechanical limitations. Clearly, further research into production–yield relationships is required.

Summary

A major challenge of ASPY was to develop reasonable estimates of potential fish production for the Great Lakes. In this paper we have attempted to address the problem through a review of methods and relevant production theory. This process led to the selection and development of methods which we considered could be applied to Great Lakes data.

In the empirical approach we have estimated yield rather than potential production because the models which form the basis of this approach are derived from yield data which are essentially "catch" and do not take into account variability in effort, limitations in harvest imposed by regulations, or biomass tied up in unharvested species. Most of the empirical models also have weaknesses associated with variability of the limnological predictors used as independent variables. Some of the models have potential for use by managers as first–order predictors, but require refinement and improved input information. The simplest model to apply, the MEI, was the best empirically derived estimator, although Lake Erie's nutrient loadings and Lake Winnipeg's turbidity and TDS loadings do not meet the criteria for its use in those lakes. It is not surprising that the MEI was closely correlated with zooplankton biomass estimates for the Great Lakes, since it describes physical and chemical characteristics which control production at the bottom of the food web.

The biomass–size spectrum model of Borgmann provides an estimate of potential production of fish larger than 17 g from invertebrate production assuming a flow-up of all biomass in the food chain. Predictions of potential fish production exceeded Matuszek's (1978) MSY (from historic yield data) by factors ranging from 2.5 for Lake Erie to 11.2 for Lake Ontario. The crudeness of these estimates is recognized because (1) zooplankton and benthic production have not been measured in each lake but instead estimated indirectly from biomass data in the literature and turnover rates measured in Lake Ontario, (2) the particle-size-conversion efficiency ($\epsilon = 0.26$) estimated for Lake Ontario has been applied to the other lakes, and (3) the model assumes no loss of biomass, i.e. all prey organisms are eaten by predators. With these limitations it is likely that the Borgmann model has overestimated potential fish production for the Great Lakes and Lake Winnipeg. Further research into invertebrate production in the Great Lakes and elsewhere is required to provide the information necessary to refine predictions from this model.

In a third approach we recognized that it may be useful to take account of finer-scale details of the size spectrum because "small" and "large" species harvested from the Great Lakes have different life history characteristics. We combined these parameters and population P/B ratios from the literature with Borgmann's model to predict potential fish production for the two size classes. From population dynamics theory, potential (or optimum) yield was calculated to be about 55% of potential production. The resulting optimum yield estimtes for large fish were remarkably close to the MEI predicted yields. Observed sustained yields of small fish obtained from commercial yield statistics ranged from only 6% of potential yield in Lake Ontario to 74% in Lake Erie. Similar ratios for large fish ranged from 21% in Lake Michigan to 100% in Lake Erie. These estimates suggest that Lake Erie is being fished at close to its yield capacity, particularly for the large taxa. The optimum yield estimates for the other Great Lakes suggest underutilization of fish resources (possibly species not currently exploited), but we recognize that detailed yield recommendations are beyond the limits of reliability of the present application.

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A Perspective on Great Lakes Fish Community Rehabilitation[1,2]

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Review of the ASPY syntheses suggested that destabilization and subsequent fish community recovery in the Great Lakes are compatible with a model in which postglacial succession, and the structure and persistence of the fish communities, were governed by piscivores. Recent advances in the areas of particle size distribution, ontogenetic niche theory, and ecosystem stability contributed to a broader understanding of fishery management alternatives. Species succession in Great Lakes aquatic communities is characterized as a cyclic repetition of maturation followed by seasonal, annual, or periodic setbacks. These are termed "enjuvenation events" and are attributed to any cultural or climatic factors which induce flux in energy–matter delivery to the system. The extent of enjuvenation is dependent upon the magnitude of the perturbation and maturity of the community and is predictable to some degree by the age and biomass distributions of the species present. The time course of rehabilitation to any arbitrary prior condition of the community is closely related to the enjuvenation–maturation cycle and to the life span and reproductive characteristics of the species present. The principal homeostatic mechanism is perceived to lie with variations in the durations of life history stanzas as affected by fish growth rates. The "biomass storage" function of larger organisms in the system is thought to be a major determinant of the "biotic inertia" or sensitivity of the community to perturbations. We are convinced that trophic linkages from the piscivores downwards must be maintained as biological feedback pathways to ensure that moderately excessive fishery yields can be self-limiting. Without these linkages (vulnerable to intensive exploitation or other catastrophic reductions in predators), biomass capture of nutrient inputs by algae will vector to waste as planktivore density limits secondary production. The extent to which the fish community can be maintained or driven to a particular species composition is dependent upon the degree of external control of all sorts that can be applied to the system. The rehabilitation continuum ranges from a self-sustaining assemblage of native species requiring little external control to a completely artificially supported community of non-native species requiring extensive controls for both water quality and fish community maintenance.

Un examen des synthèses de l'ASPY porte à croire que le déséquilibre de la communauté piscicole des Grands Lacs et son rétablissement ultérieur concordent à un modèle où la succession post-glaciale ainsi que la structure et la permanence des communautés piscicoles sont réglées par les piscivores. Les récents progrès réalisés dans les domaines de la répartition de la taille des particules, la théorie d'une niche

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ontogénétique et la stabilité des écosystèmes ont mené à une meilleure compréhension des différentes méthodes de gestion des pêches. La succession des espèces dans les communautés aquatiques des Grands Lacs est décrite comme une répétition cyclique de la maturation suivie de reculs saisonniers, annuels ou périodiques. Ceux-ci sont appelés des «événements d'enjuvénation» et sont attrribués à tout facteur cultural ou climatique qui occasionne un flux de l'énergie–matière libérée dans le système. L'amplitude de l'enjuvénation dépend de l'ordre de grandeur de la perturbation et de l'état de maturité de la communauté; de plus, elle peut être extrapolée jusu'à un certain degré la distribution des âges et de la biomasse des espèces présentes. Le déroulement du rétablissement de la communauté à tout état arbitraire précédent est étroitement lié au cycle enjuvénation–maturation, à la durée du cycle vital et aux caractéristiques de la reproduction des espèces présentes. On croit que le principal mécanisme d'équilibre homéostatique est imputable aux variations de la durée des partitions du cycle vital telle qu'influée par les taux de croissance des poissons. On considère que la fonction «d'entreposage de la biomasse» par les gros organismes du système est un important facteur déterminant de «l'inertie biotique» ou de la sensibilité de la communauté aux perturbations. Les auteurs sont persuadés que des liaisons trophiques entre les piscivores et les niveaux inférieurs doivent être maintenues à titre de processus biologiques de rétroaction afin d'assurer que des rendements de la pêche modérément excessifs soient auto-limitatifs. Sans ces liaisons (vulnérables à une exploitation intensive ou d'autres baisses catastrophiques du nombre de prédateurs), le captage massique de bioéléments par les algues sera en vain car la densité des planctivores limite la production secondaire. Le point jusqu'à lequel la communauté piscicole peut être maintenue ou amenée vers une certaine composition spécifique dépend du degré de contrôles externes de toutes sortes qui peuvent être appliqués au système. Le continuum du rétablissement varie d'un assemblage auto-suffisant d'espèces indigènes nécessitant peu de contrôle externe à une communauté totalement allo-suffisante d'espèces exotiques nécessitant des contrôles considérables en vue de maintenir la qualité de l'eau et d'assurer l'existence des communautés piscicoles.

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The focus of the International Symposium on Stock Assessment and Yield Prediction (ASPY) was to examine fish production processes to determine how best to allocate production from degraded fish communities to the special needs of rehabilitation, to community maintenance, and to human utilization. The purpose of this paper is to develop a conceptual framework that will encompass the changes that have occurred in the fish communities of the Great Lakes and that will allow prediction of events likely to be observed as fishery rehabilitation progresses. The ASPY challenge has been to attempt to develop the kinds of models Orians (1975) called for, i.e. useful at a level of analysis intermediate between general models of community ecology and management models of single-species fisheries. Some of the existing models (e.g. age-structured dynamic pool models) have been used for Great Lakes fishery management in spite of known inadequacies, and this has been appropriate during the recent past while we have been developing an understanding of the extent to which Great Lakes fishery productivity might be restored or rehabilitated. There is general agreement among Great Lakes fisheries workers that today we are confronted with an impressive array of opportunities for providing interesting and valuable fisheries in the Great Lakes. Realization of these opportunities will depend on accurate assessment of the status of the ecosystem and development of fishery management measures that will recognize the dependence of the fisheries on the productive capability of the ecosystem.

By "rehabilitation" we mean a reversal (not merely an interruption) of degradation of the biological productivity of the fish community, where "productivity" is broadly defined by human evaluation of the biotic products. This does not suggest reversion of the ecosystem to some primeval state that would exclude human utilization, but rather an incremental recovery of the ability of the system to sustain valuable fish production throughout the foreseeable future. We contend that a reasonable minimum expectation would be a genuinely sustainable yield approaching the level of fish production enjoyed throughout the 1920's and 1930's in the upper Great Lakes, with a species mix comparable in value with that of the earlier period. Such a level of production is clearly possible and in some locations is already being achieved, hence our conviction that fisheries management authorities should settle for no less. Present estimates of Great Lakes fish production and yield (Leach et al. 1987; Lewis et al. 1987; Loftus et al. 1987) show that the separate approaches have converged significantly, and by so doing have exposed an interesting difference, which is discussed below. Earlier discussions (Christie 1978) about the possibilities of increasing yield by cropping at lower trophic levels are no longer relevant in an era where the focus of management attention is on the harvesting of rehabilitated walleye (*Stizostedion vitreum vitreum*) and salmonid stocks. In the long-term context, therefore, present debates about levels of allowable catch appear of minor significance when compared with the earlier ones which concerned the very basis of regulatory management. What has particularly enriched the new understanding are the examples of ecosystem linkages which demonstrate important new ties between water quality and fishery management. We are convinced that Great Lakes management directed at maintaining or enhancing ecosystem health will minimize control costs in the long term, including costs associated directly with fisheries and with the major issues of water quality. Our optimism rests upon previously published historical accounts of Great Lakes fisheries and the exposition at ASPY of recent advances in ecological theory that will enable more accurate prediction of ecosystem development as fish community rehabilitation proceeds.

The conceptual model described below is an attempt to interpret, at the level of the Great Lakes fish community, ecological theory developed in connection with particle size spectra (Sheldon et al. 1972), ontogenetic niche (Werner 1984),

size selection (Dodson 1974), community succession (Margalef 1968; Odum 1969; Holling 1986), the "storage principle" (Patten 1985), and the harmonic community of Ryder and Kerr (1978). We offer this interpretation as an illustration of our conviction that fisheries managers are now in the position of having powerful theoretical models to apply to the problem of predicting ecosystem behavior (see, in particular, O'Neill et al. 1986).

We build upon two observations that emerged from the International Symposium on Salmonid Communities in Oligotrophic Lakes (SCOL, Loftus and Regier 1972). First, homologous guild structures characteristic of the holarctic oligotrophic lakes represented community patterns that were evidently resistant to change with time (W. J. Christie and K. H. Loftus, unpubl. data) in spite of varied, and in some cases extreme, variations in climatic and other conditions of the physical environment. The species differed between European and North American lakes, especially, but taxa within the major feeding "guilds" on each continent showed considerable similarity. Presumably, these communities were repeatedly challenged by other potential colonists (including the recently established exotic fish of the Great Lakes) through the interglacial years, but the established taxa were able to resist the challenges. The mechanistic reasons for the resistance of these communities to invasion or establishment of exotic organisms may be the "congeneric homotaxis" of Hill and Durham (1978) or the "taxocene" of Chondrowski (see Regier 1970). This emergence of homologous Old World and New World communities from differing arrays of postglacial colonists represents a form of succession, and W. J. Christie and K. H. Loftus (unpubl. data) suggested a set of assembly rules (Diamond 1975) which may have governed the patterning processes.

The second SCOL observation was that degradation of the salmonid communities in response to fishing, cultural eutrophication (not to be confused with natural lake ageing on a geological time scale), and introduction of exotic species results in similar changes in the fish communities (guild shifts in our current terminology) irrespective of the origins of the perturbation. A strong literature has since developed to characterize this general ecosystem pathology (e.g. see Rapport et al. 1981, 1985). This common stress response suggests that some fundamental principles of ecosystem organization govern community development in response to strong environmental perturbations. Implicit in our approach is the understanding that degradation of aquatic ecosystems is a reversible process. Presented tentatively at the SCOL symposium nearly two decades ago in connection with the "oligotrophication" process, this understanding has clearly been extended to nearshore regions within the Great Lakes basin, e.g. Bay of Quinte (Minns et al. 1987), Long Point (Regier et al. 1980), and Green Bay (Harris et al. 1982). We believe that the ASPY case histories provide further documentation of broad ecosystemic responses to fishery exploitation, environmental changes, and species interactions.

The long time scales involved in the dynamics of fish communities are peculiarly significant in relation to understanding ecosystem processes. As with evolutionary theory, the slow processes require reliance on homology for the development of understanding and predictive capability (Gould 1986). Unlike evolution, however, identifying ecosystem homologies requires considerable attention to methodology. Also unlike evolution, serial homology can be examined as well as spatial homology, albeit over long time intervals, and in both circumstances, methods must be rigorously comparable. This is not a simple matter. The history of fish population dynamics reveals substantial success with serial homology for individual fisheries and a somewhat less successful record in the area of population comparisons. At the ecosystem level, methods which can be compared or calibrated will relate in part to the descriptors chosen, and both require extensive collaboration between scientists. One of the strongest lessons from ASPY, and earlier from SCOL, has been the demonstration of a continuous need for research and management information integrated at several levels of resolution so that comparisons and contrasts between aquatic ecosystems can provide a basis for prediction of future events, given an appropriate conceptual framework. We submit that useful predictions of community change may be made even without detailed knowledge of individual species responses. The conceptual model presented below provides a basis for judging progress toward any arbitrary rehabilitation objective in terms of external controls necessary for community maintenance.

Some Succession Theory

Ideas about succession have evolved significantly from the classical Clementsian forest succession model taught to generations of ecology students. The concept of progression to a "climax" state has been replaced by the "shifting mosaic steady state" of Bormann and Likens (1979), depicting forest biomass developing to average levels substantially below the maxima.

Understanding succession has been hampered by insufficient consideration of all the trophic components of ecosystems and by excessive attention to brief temporal segments of the process, as with old field succession studies (e.g. Minkler 1946). These limitations were understood by Margalef (1968, 1975) and Odum (1969), who interpreted succession as ecosystem development, i.e. an "increase in internal links" in the ecosystem, and suggested that linkages between primary production, grazers, and predators can be measured in terms of system maturity. These workers, and especially Odum et al. (1979), also introduced the concept of perturbation impacts on ecosystem development, and subsequent workers (e.g. Vogl 1980) have recognized ecosystems which are perturbation dependent. We assume that perturbation of aquatic systems consists of flux in energy-matter and that the species pathways (structures) and magnitude of fluxes define ecosystem development. To understand the effects of perturbation, both cultural and "natural," it is necessary to identify a scale of common units. We subscribe to the idea of "enjuvenation" (W. J. Christie and K. H. Loftus, pers. comm.) as a useful descriptor of the process described in early ecology texts as "successional setback." Unlike "rejuvenation," it clearly establishes the direction in which ecosystem maturity has moved without requiring that a specific state (juvenescence) be achieved by the action of the perturbing force. We believe that enjuvenation is one of the key features influencing vulnerability of ecosystems to invasion of nonendemic species.

In terrestrial systems, forest fires, blow-downs, disease, and insect pest outbreaks enjuvenate by allowing surges of solar energy to reach the ground through holes in the forest canopies (Vogl 1980) and by returning nutrient materials for use by organisms more characteristic of earlier succession stages. The concept is also applied to savannas which are enjuvenated by fire and browsing. There is debate about the regularity with

which this patchy enjuvenation proceeds, but no disagreement on the point that average level of maturity is always below the maximum.

We suggest that there is an aquatic analogue for these terrestrial enjuvenation events that places cultural and natural stresses in a context useful for predicting ecosystem development and that is mediated by meteorological events which provide natural enjuvenation opportunities, at least in temperate zone ecosystems. Lake systems are better buffered against climatic extremes than terrestrial ones, but the most vulnerable areas are the shoals, littoral zone, and tributary streams, and impacts on these areas have disproportionately large effects on the fish communities. Large storms alter physical habitat in major ways. While extremes in these episodic events appear superficially to jeopardize entire stocks of river-spawning lake fish by elimination of fish and their food in streams, the semiannual regularity of the equinoctial gales clearly plays a role in maintaining the succession of generations for many of the larger Great Lakes fishes. The extensive use by salmonids of these exposed shoals as spawning habitat during the most tempestuous seasons clearly indicates their dependency on the physically enjuvenating effects of storm scouring to provide a "pioneer" community environment for eggs or larval fishes which do not enjoy parental protection. Water level variations have the same effect of exposing the littoral zone to varying degrees of wave and current action, but the energy pulses extend over both annual and longer cycles. Watershed erosion from seasonal episodic events including forest enjuvenation and from the longer term precipitation cycles causes nutrient surges which are also enjuvenating.

Fishing produces enjuvenation effects by reducing the abundance of long-lived components of aquatic ecosystems. Exactly how the maturity levels are measured matters, and this may have been an impediment to progress in development of the concept. The measures suggested by Odum (1969), like the production/biomass ratio (P/B), show very little shift in response to fish community enjuvenation when averaged at the system level because of the relatively greater biomasses found at the lower trophic levels. This is an illustration of the point made by Patten and Odum (1981) that organisms occupying positions near the apex of the Eltonian Pyramid of numbers can influence community structure and function to a degree disproportionate with their relative biomass, or contribution to community metabolism. This accounts in part for the attraction of contemporary workers to particle size theory (Sprules and Munawar 1986; Borgmann 1987; Minns et al. 1987). A related approach was suggested by Patten (1985) who noted that living organisms store energy in direct proportion to their own biomasses and Margalef (1985) who noted that this storage (information content) relates inversely to turnover, i.e. is proportional to B^2/P. This is important if Margalef's assertion is correct that the degree of indeterminism in an ecosystem and its direction of future development are functions of the ability of individual organisms to store energy. Margalef's approach is also appealing because it addresses a question of vital concern to resource managers (and a focal point for ASPY): how the generation times of species in a fish community relate to its future development. The issue is further explored in Patten (1985) and May (1986) and the emerging concensus is that the long-standing generalization that roughly 10% of the energy at one trophic level survives to reach the next higher level should be discarded in favor of recognition of the role of storage and indirect linkages in slowing the dissipation of energy from ecosystems. Our interpretation of these ideas is that the enjuvenating effect of fishing acts through reductions in storage components and in the time-integration capacity of the fish community. Taken to excess, the fish community will exhibit the classical symptoms of overfishing.

Cultural eutrophication is an exaggerated case of energy-matter surge. The natural cases of annual deliveries of allochthonous nutrients by freshets and of autochthonous nutrients by the vernal and autumnal turnovers of lakes are also enjuvenating, but differ in scale and duration. Odum (1971) discussed the slightly more dramatic impact of energy surge induced by tidal maxima on salt marshes. The time-scale in which nutrients are supplied to aquatic systems is a critical determinant of the cultural eutrophication impact. Inputs can range from the almost continuous injections of phosphates (typical cultural eutrophication) to the less regular but still frequent impacts of winterkill in some northern lakes (Tonn et al. 1983). Juvenescence is sustained in both cases because there is insufficient time for organization, in the same way tundra communities are held at low levels of maturity by the brevity of the growing seasons (Margalef 1968). Both these cases involve anoxia as a consequence of insufficient time-integration capacity of the aquatic community. We would predict that the end results of overfishing on a fish community would be similar. On the eutrophication side, quantities of nutrients in excess of what the system can handle bring about the short-circuiting of system development, and on the other, holding nutrients constant, but disrupting energy flow by catching off large fish, can produce excess algae (Spencer and King 1984).

Fish species composition is affected by the distribution shifts induced by long weather cycles and trends (W. J. Christie and K. H. Loftus, unpubl. data). Short-term weather effects are known to influence reproductive success for a number of species, and the connection is suspected for others. The dramatic shifts in species dominance in the Great Lakes, in fact, were on this account considered almost entirely under the control of exogenous influences for many years. Our interpretation is that for any species population which is adapted to exist within a specific range of climatic conditions, the effects of a series of poor years for reproduction are to reduce stock density and advance mean age. For the species in which weather – year class strength correlations have been demonstrated, and which occupy terminal positions in their food chains (smallmouth bass (*Micropterus dolomieui*), lake whitefish (*Coregonus clupeaformis*), walleye), it is safe to predict that ecosystem maturity drops as their density is reduced. Production of a large year class when weather is again suitable for these species will advance system maturity as stock biomass develops, but it is important to note that this is not an instantaneous effect. Enhanced survival of larval fish of a particular species temporarily depresses system maturity as measured by mean age. Only as the biomass of that year class ages and becomes concentrated in older fish (in Margalef's terms, as the system accumulates information) will the system maturity increase; numerous progeny from a particular hatch merely provide an ecological opportunity for gains in system maturity. With subterminal species such as alewife (*Alosa pseudoharengus*) (Henderson and Brown 1985) and yellow perch (*Perca flavescens*) (Henderson 1985), climatic effects are probably more readily discerned at low piscivore densities, but in general, reduced density in such species acts to advance community maturity.

An important result of this theory is the prediction that compensatory responses should be greatest for communities well below mean maturity levels (Margalef's (1975) "highly reactive" system) as is the normal case at the population level. The reverse should be true for situations where maturity exceeds the mean. This may be the reason for the apparent lag in effect of the intensive fishing of the last century, where massive yields of Great Lakes species continued unabated for decades, only to result in population collapses over very short time intervals once the exploited stocks approached some uniform minimum mean size at maturity and a correspondingly low level of system maturity. This hypothesis is consistent with the frequent observation that the most dramatic year class production for many species, e.g. blue pike (*Stizostedion vitreum glaucum*) in Lake Erie and whitefish, lake trout (*Salvelinus namaycush*), and sea lamprey (*Petromyzon marinus*) in Lake Huron, occurred when system maturity was low because of a major enjuvenation event. In the cases above, the respective events were overexploitation (Regier et al. 1969), the 1942–43 die-off of rainbow smelt (*Osmerus mordax*) (Van Oosten 1947), and the collapse of lake trout stocks due to lamprey predation and fishing (Fry 1953; Berst and Spangler 1972). We should then expect the greatest increases in variation of year class strength just before population collapse.

Aquatic systems are not so clearly prone as their terrestrial counterparts to the cyclic enjuvenation associated with advanced maturity (Holling 1986). Removal of the old fish by disaster may enhance the enjuvenating effect of an energy surge, in some cases, but it may more often be the case that conditions at or below the climatic norm for a region over a series of years predispose aquatic systems to enjuvenation by producing low recruitment to the maturing fish community, thus enhancing the effect of a high energy surge when it occurs. The phenomenon is difficult to study because most such systems are exploited, and the reduced biomass of old fish enhances year class irregularities. A few cases, such as the single year class dominance reported by Alm (1951) for European perch (*Perca fluviatilis*) and the Keller Lake lake trout and whitefish (Johnson 1972), suggest endogenous rhythms like those reported for terrestrial systems. The question is an interesting one deserving attention.

As noted above, the effect of traditional fishery exploitation (i.e. pursuit of a maximum sustainable yield (MSY) objective) is to reduce system maturity, thus allowing opportunistic species a chance to benefit from the (temporary) availability of resources freed by enjuvenation. This phenomenon probably accounts for the widely differing results of deliberate and accidental introduction of exotic organisms into new environments. The attempts to establish Pacific salmon in the Great Lakes late in the nineteenth century (Parsons 1973) met with little success because the fish communities of the day included enough larger, older fish to keep system maturity at relatively high levels. Similarly, the Lake Michigan alewife die-offs of the middle 1960's predisposed the communities for favorable production of larger and longer-lived species. This should be testable in retrospect, with conspicuously higher survival rates of salmon and lake trout immediately following major die-offs of smaller species. The process is entirely predictable, even if the resulting species composition is itself a simple accident of timing, as for whitefish in 1943 (Hile and Buettner 1959; Budd and Cucin 1962; Lawler 1959), lampreys in the 1930's, and salmon and lake trout in the 1970's. The structural question of which species will succeed in dominance after a particular enjuvenation event may be a matter of "supply-side ecology," a term attributed by Lewin (1986) to J. Roughgarden to identify the elements of community organization that depend on the entry of new organisms. Thus, the colonization of Lake Superior by the pink salmon (*Oncorhynchus gorbuscha*) (Schumacher and Eddy 1960) was a manifestation of the extreme reduction of system maturity accompanying the lake trout collapse.

We view viable communities as species aggregations exhibiting some of the properties of individual organisms, but capable of interrupted maturation and indefinite life span. Interaction between species is obviously necessary, but the guild-structured concept of community requires coadaptation among species only at the elementary levels of adjustment described by Svardson (1976). This allows for significant species change in response to major climate or other environmental changes.

System Maturity in the Great Lakes Context

It has become customary to distinguish the primary phases of succession from the secondary succession associated with recovery from disturbance (McIntosh 1980). The distinction is seen as important because it is implicit in all harvesting theory for forestry, wildlife, and fisheries that human society takes advantage of the compensatory responses of communities in secondary succession. Agriculture represents an extremum on this scale, in which production systems are carefully controlled at or very near a perpetual "pioneer community" state through massive inputs of external resources (plowing energy, herbicides, pesticides).

It would be convenient if "secondary succession" only referred to situations where relaxation of a stress or completion of a disturbance is followed by natural recovery. Unfortunately, the point of damage beyond which intervention is essential is often not readily seen, and even if it is, natural recovery time scales are often known, or perceived to be, excessively long. It impresses us that the Margalef–Odum concept of ecosystem development espoused here is preferable because it avoids this definition problem.

Holling (1973, 1986) and his co-workers have developed a community concept which allows for multiple steady states. In this construct, a sufficiently severe disturbance can move a system from one "domain of attraction" to another. Domains are maintained by thresholds and breakpoints which act to impede the natural maturation sequence. This is consistent with the SCOL guild model and with Margalef's (1975) "essence of maturity." If a perturbation is such as to eliminate the piscivores in a system, for example, the guild structure will obviously not be naturally restored. Even without extinction, the distortion of the predator-prey balance can be sufficient to allow the prey to prevent recovery of the piscivores (witness the indefatigable efforts of fishery managers to "balance" largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*) ratios in ponds and small lakes). The Great Lakes experience has been that even though the fish communities were scarcely stable during and after degradation, no regular increments in system maturity occurred until piscivores were reintroduced. The most urgent need is for definition of the limit to which system maturity can be reduced without endangering its capacity for subsequent maturation.

Figure 1 is a schematic of our concept of ecosystem development in the Great Lakes as reflected by the fish communities. Obviously the time span for the organization phase is arbitrary relative to the rest of the diagram, and both

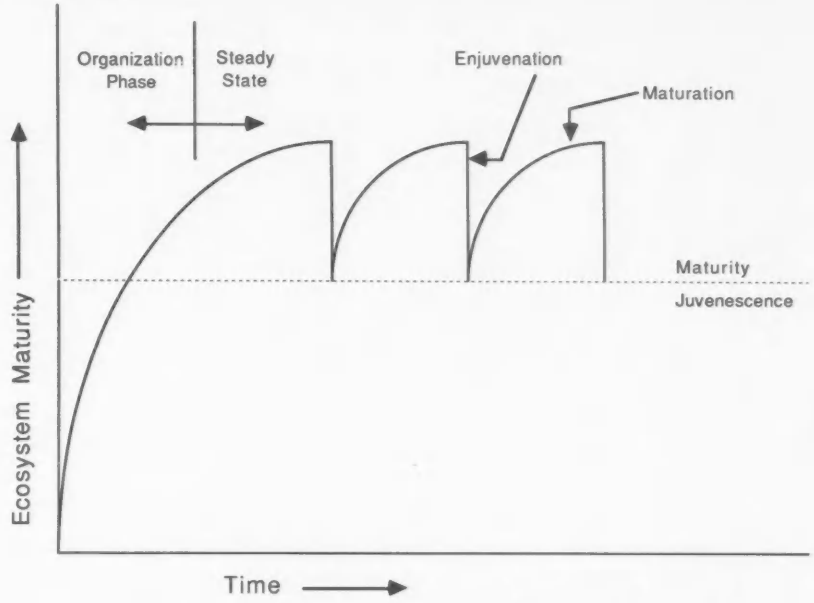

FIG. 1. Schematic to illustrate succession processes in an aquatic ecosystem.

amplitude and frequency of the perturbation–recovery notches are equally imaginary. We would predict, however, that a similar diagram representing tropical systems would have lower amplitude and frequency (and perhaps a somewhat higher placement in the figure overall) because of the relatively greater constancy of insolation. We note that our depiction is similar to Odum's (1971, fig. 4.1) illustration of ecological succession, although we believe it unnecessary to provide for an "ageing" stanza. The "sawtooth" nature of the process is important because it emphasizes the nearly instantaneous nature of the enjuvenation events, followed by redevelopment of system maturity at rates that are state dependent. An important prediction from the figure is that amplitude of the notches should decrease as the line is extended to the right in evolutionary time.

Relatively speaking, all Great Lakes fishes are generalists. This is a consequence of the disruptions of the glacial epochs and because there has been insufficient time since the retreat of the Wisconsin Glacier for species elaboration. Lake Baikal is the only studied north temperate zone oligotrophic lake which has escaped glaciation, and its example tells us that coevolution is manifest in significant speciation, together with its complementary niche elaboration, various kinds of mutualism, and other adaptations that characterize emergence of new species (Kozhov 1963). We raise this point particularly to support our guild concept. Ryder and Kerr (1978) suggested that harmonic communities are defined as integrated, persistent, and consisting of coevolved species. We believe that Great Lakes fish communities were integrated and persistent, but the species can only be considered coevolved in the very broadest sense.

Biomass versus Life Span Relationships

The question of time scales in ecosystem development has been a recurrent subtheme throughout this essay, and it warrants delineation. The principal generality is that the minimum time step for characterization of ecosystem maturation would be the length of a generation for the longest-lived members of the system. Defining this technically (the *G* of Krebs 1978) as the mean time elapsing between birth (or colonization) of parents and the birth of offspring, we suggest that in practice it probably requires more than a single generation for the long-lived fish to establish densities appropriate to sustainable community structure. In theory, therefore, continuous restocking of lake trout in the Great Lakes has the function of infilling year classes to build biomass before the completion of the first *G* (approximately 15 yr in this case) and providing continuous juvenile output thereafter. With long-lived fish, even very low survival to recruitment to the adult stock can ultimately accrue sufficient predation power to develop control (Johnson 1973). From this we infer that a lake trout system can be considered juvenescent beyond some point where losses of eggs or young fish reduce recruitment to the spawning stock sufficiently to prevent increase of a reduced stock of the trout. The time frame is critical to the juvenescence definition. As we suggested above, overfishing a recovering brood stock can effectively permanently stall the rehabilitation process.

At the other end of the ecosystem scale, recent events have illustrated the speed with which large-scale system responses take place. Algal densities respond promptly to changes in phosphate loading (Minns et al. 1987). They also react quickly to changes in planktivore densities by way of shifts in zooplankton composition and abundance (Edgington 1984). At least in part, the reason that only the early, but not the final, results of the massive eutrophication control programs of the 1970's have been observed is that there has not been sufficient time for the full recovery of the long-lived fish. In the case of lake trout in the upper Great Lakes, it is likely that there may not yet have been sufficient time for the fish to gain predatory control over the system.

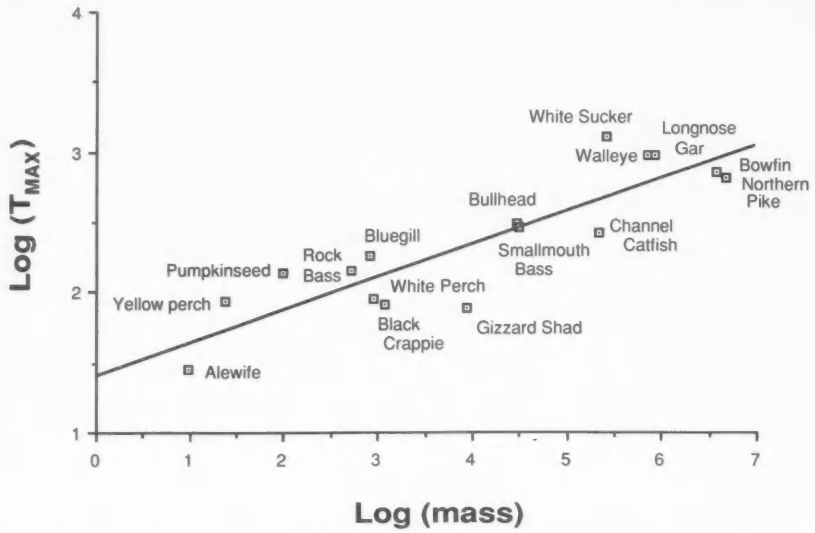

FIG. 2. Relationship between mean body size (grams) and maximum age (years) for 16 species of freshwater fish.

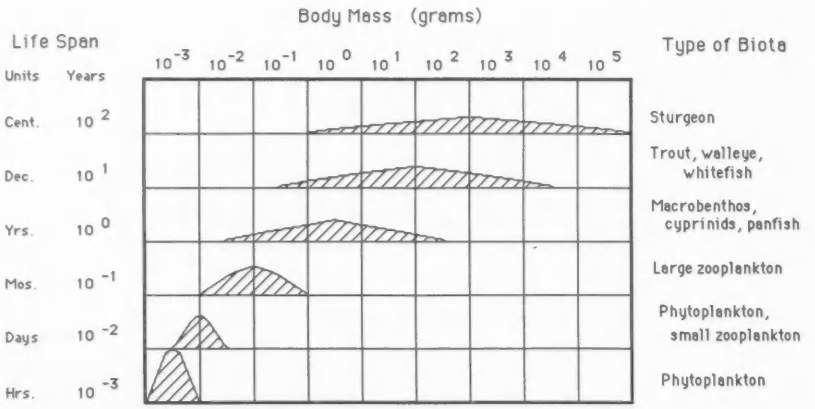

FIG. 3. Hypothetical distribution of biomass in organisms of various life spans in a freshwater community.

It has long been realized that there is a strong positive correlation between body size of organisms and generation time (Bonner 1965). In linear dimensions, organisms ranging in size from bacteria to giant sequoias show a clear log–log relationship to generation time scaled from minutes to years (Bonner's fig. 1). The relationships between various physiological rates, body size, and longevity have also been explored extensively in recent years. Calder (1984) defined allometries for longevity and mass for birds, mammals, and reptiles, and the exponents all lay between 0.19 and 0.23. We are not aware of published examples for fish, but from archival data at the Glenora Fisheries Station (R.R. No. 4, Picton, Ont. K0K 2T0), we computed

$$T_{max} = 4.14M^{0.23}$$

where T_{max} was computed from mortality estimates at standardized sample size after Hoenig (1983, appendix equation 2) and M is the average weight for a species population computed over all age classes. The regression (Fig. 2) described 16 warmwater species across the range 3 g (alewife) to 700 g (northern pike (*Esox lucius*)), and it clearly suggests that they share a common exponent with the other vertebrates. For the Great Lakes aquatic ecosystem, we assume that biomass is approximately constant over logarithmic size classes (Sheldon et al. 1972), that longevity is broadly predictable from the mass attained by the animals, and that individual species have upper limits for size and age that are well defined within a climatic zone. It follows that the successional status of a particular community can be known roughly by the age/biomass distribution of its component species.

Figure 3 illustrates how ecosystem biomass would be distributed among the organisms in a Great Lakes aquatic community. Here the areas below the curves in each row sum to

unity, and the modes for the age classifications (body masses) advance according to the exponent 0.23. We had no data for the longevity–mass relationship in the invertebrate classes and assumed that it followed the same law. The curves are symmetrical and drawn with variances proportional to means, in the absence of contrary evidence.

Interactions between organisms in the various columns may be predator–prey linkages, while within columns, organisms of similar size may interact competitively; however, the argument does not depend on such direct linkages. It is interesting to note that while size spectra are hard to determine for natural systems because of the difficulties in calibrating gears used to collect across the broad range of organism sizes, it may be easier to develop age spectra within the columns.

We believe that this construct can be used to depict distributions for the ecosystem properties Odum (1969) described as useful descriptors (P/B, respiration, production, etc.), and each should yield a characteristic surface. The surface will vary according to the position of the system or fish community within an enjuvenation–maturation cycle, and the boundaries for natural variance can be quantitatively defined over the variety of system/community types. Equally, it seems likely that perturbations which drive the systems below the juvenescence line in Fig. 1 will be readily identifiable by major distortions of the surfaces.

The addition of the age dimension to the conventional Sheldon spectrum has a few potentially important advantages. The elasticity of fish growth rates represents an important equilibrating mechanism (see below) which can at least temporarily mask trends towards pathological structural change in simple size distribution analysis. The age of the organisms embodies their lifetime experience in the system, including some behavioral phenomena such as learning that are extremely difficult to quantify but inevitably contribute to the overall functioning of the ecosystem. Prey imaging and predatory switching (or lack of it) are likely to be more closely related to the age (experience) of the predators than to their sizes. This may be an element of the concept of storage defined by Patten (1985), who suggested that the longevity of an organism may be more important than its mass, in terms of its role in the ecosystem.

We suggest that Fig. 3 provides a qualitative diagnosis of the "storage" or "biotic inertia" of the system. In practical terms, the qualitative disaggregation of the figure allows managers to distinguish emergence of dangerous structural conditions in terms of real organisms, and this is critical to remediation.

Resilience and Homeostasis

If the guild structure of Great Lakes fish communities is a valid model for what we have seen during this past century and if ecosystem development occurs approximately along the lines that we have presented, then it is possible to make some strong inferences about the way the system will behave with respect to predator–prey dynamics. We might also infer how species with different life history strategies, especially along the r–K reproductive continuum, might behave in this system.

The concept of "r" and "K" selection developed by MacArthur and Wilson (1967) requires a mechanism or mechanisms to permit recovery of competition-adapted K species after a disturbance has reduced their numbers relative to the more reproductively effective r species. As W. J. Christie and K. H. Loftus (unpubl. data) pointed out, there have been two hypotheses offered for fish communities. Pianka (1970), on the one hand, suggested that all fish occupy the same small segment of the r–K continuum, while Murphy (1968) proposed what amounted to a redefinition. This was based on his observation that longer-lived clupeids showed higher reproductive variability than the shorter-lived members of his series, suggesting that they possessed capabilities for prompt recovery following disturbance. Our hypothesis by contrast accepts the r–K idea and an unmodified classification for fish within it. We suggest that the "size efficiency hypothesis" as defined by Dodson (1974) is especially applicable to fish because of the phenomenon of the "ontogenetic niche" (Werner 1984), especially as viewed dynamically from the perspective of predation risk. Dynamism does not affect the generality of the r–K balance question, but it enters the discussion of homeostasis below. The central idea is that small (r-selected) fish species are vulnerable as prey through their usually short lives, while the K-selected fish have relatively brief periods of vulnerability to predation. As noted above, the long life spans ensure that even very low survival past the predation threshold leads to accumulation of the K fish towards significantly large spawning biomass. To the extent that these species are primary or secondary piscivores (Keast 1983), this accumulation imposes increasing control over the r species (see also Holling 1986 for further discussion). This is an illustration of Patten's (1985) storage principle and an interpretation of how biotic inertia can be expressed in the reproductive potential of the community.

The ontogenetic niche concept implies stepwise progression in the life histories of fishes, and to the extent that the range of sizes of zooplankters (for example) tends to be well separated from the size distribution of the benthos, the generalization may be useful. Within the fish trophic tiers, the progressive selection of larger prey, as the predator grows, seems to be the rule (other things being equal), even though there are major shifts in the prey species selected through the progression. Werner (1984) recognized that the concept applies to stanzas of vulnerability to predation as well as to the feeding stanzas, but we argue explicitly for a continuous size selection process, interrupted only where breaks in the prey size or predator size distributions occur. This concept is close to "metaphoetesis," as defined by Hutchinson (1959) and developed by Kerr (1974), but we have retained the term ontogenetic niche because of its currency.

The importance of the concept lies in its potential as an homeostatic mechanism. It has been a general observation that slow-growing fish tend to live longer, and vice versa (Beverton and Holt 1959; Pauly 1980). These studies demonstrate that the growth response is far the more important of the two, indicating that biomass equilibration in fish stocks is mainly accomplished through growth variation. When a predator depletes the prey in the optimum size range, it moves to smaller prey at a higher energetic cost reflected in reduction of the growth rate (Kerr 1974); hence, examples of stunting caused by intraspecific competition are commonplace. When fish of Keast's (1983) secondary piscivore group are stunted, the effect is to reduce the biomass of its members surviving to enter the piscivore ranks and to extend the period of planktivory in the early life history. It is more speculative, but plausible, that heavy cropping of the zooplankton in turn limits larval survival to move the biomass back towards normal densities. Similarly, reduction in primary piscivores can, we suggest, cause stunting in the middle ranges, while improved growth in the primary piscivores enhances their cropping effectiveness. We suggest that the addition of secondary piscivores to the primary piscivore biomass can occur

quickly and has the potential to be an important equilibrating mechanism.

A further generality emerging from these two concepts is that fish which are confined only briefly to the size ranges where they are most vulnerable to predation are probably less in need of the *r* strategy for their persistence. This is a strength which might serve to explain why the chubs (*Coregonus* spp.) have been able to proliferate in the upper Great Lakes in the face of burgeoning stocks of piscivorous salmonids, while the alewife has not fared so well (Eck and Wells 1987).

The *r–K* theory is relevant to the question of control of the fish community. It is no accident that all important Great Lakes native fish taxa are iteroparous (in contrast with the semelparous Pacific salmon), requiring more than a single spawning to replace the parental stock. So too are the invading species that have become self-sustaining. Note that we include sea lamprey here because their "style" of iteroparity is to invest substantial energy in larval stages that transform over a protracted period of time (up to 11 yr, Manion and McLain 1978), thus spreading the reproduction of a single year class of parents over many years. We concur with Christie and Regier (1972) that sustainability of a particular suite of species must be closely tied to a reproductive control investment that crosses a number of years. This is yet another reason why the traditional MSY approach to management (Larkin 1977) fails to provide reasonable probabilities for sustenance of even a single species. Collapsing the breadth of the age distribution of spawners for iteroparous species clearly limits the opportunities for such species to recover from otherwise benign enjuvenation events such as those due to local weather.

Some Conspicuous Consequences

It is customary in a symposium volume to single out the implications of the scientific findings for resource management. The situation here is analogous to the aftermath of the SCOL symposium in that an important conclusion to be drawn from ASPY is that the large, intractible questions which face management in the long term are intimately tied to the most difficult questions in community ecology. The lesson from these symposia is that questions about yields, optimal species blends, human impacts on the fish community, and sustainability of the resources can ultimately be dealt with only by means of greatly improved knowledge of system dynamics. The requisite knowledge increases slowly and irregularly, and we would be remiss in management of our resources if we knowingly were to defer action until some predetermined "level of understanding" had been achieved. In the following, therefore, we discuss the implications of our synthesis, in terms that we hope will be useful for both management and future research. While it is necessarily speculative, we have attempted to present a "conservative view" which, if subsequently found to be seriously in error, will, in our opinion, err "on the side of ecosystem health" so far as we can judge it at present. Thus, we acknowledge the existence of, but do not elaborate on, those management options that are not clearly sustainable, or that permanently reduce the spectrum of future management alternatives.

Ecosystem development is discussed above because we believe that many of the important issues facing ongoing management of the Great Lakes fisheries relate to the concept of succession in ecosystems and fish communities. Following the extremes of fish community degradation chronicled in the SCOL symposium (Loftus and Regier 1972), there was a general acceptance, if not concensus (Smith 1968), of the ideas that (1) even if equilibration of the sea lamprey – lake trout systems (as had existed earlier in Lake Ontario, and, perhaps, New York's Finger Lakes) occurred by way of natural mechanisms, the loss in harvest would be intolerably high for too long and (2) even where lake trout stocks had survived the sea lamprey crisis, their potential for restoring lakewide populations in usefully fast order was too limited. Thus, the decisions to undertake programs to actively control the lamprey and reintroduce lake trout contained the tacit assumptions that natural successional and equilibrating processes, if they existed at all, were too slow for societal purposes. This is a compound issue, not strictly limited to the rapidity of attaining an equilibrium condition, but including as well the general concerns associated with managing under a cloud of uncertainty. We believe that these issues can be effectively disaggregated by stipulating the management alternatives appropriate to prediction for short-, moderate-, and long-term time horizons, a key question posed to ASPY symposium participants.

In the short term, managers have no alternative but to proceed on the basis of the best (albeit flawed) models available. When the models are approximately correct, but parameter estimates are imprecise (or lacking), the "adaptive or experimental management" approach (Walters 1986) provides a powerful technology for successive improvement in managing toward the model objectives. An alternative is to settle for imprecision in parameter estimates and apply vulnerability analysis (Vincent 1981; Cohen et al 1987) in order to explore just how sensitive the existing system is to strong perturbations. The former approach relates at least to near-term prediction whereas the latter might be applied to questions of interest over a somewhat longer time frame. This might provide for the development of an optimal controller, given some bounds on the magnitude of possible perturbations (Vincent 1987).

Both of these approaches require that our management model be approximately "correct" in the sense that overall system behavior be reasonably well known. This applies as well to the economic models that provide for evaluation of biological production from the fish community (Milliman et al. 1987; Hanson 1987). Major uncertainties arising outside the bounds of the system (as described in the management models) make the long-term prospects for management completely unpredictable. This is not a flaw in these approaches, but rather a more basic failure to continue to amend and improve our understanding of ecosystem behavior simultaneously with our exploitation of the system. Clearly, this is the *raison d'être* for maintenance of a research function at every level of organization within the ecosystem and the substance of Allen's (1985) contention that "...interacting populations should be studied in the context of a 'space' larger than that [occupied] at a given instant." We maintain that the best insurance against unpleasant surprises in the distant future is to manage in the direction of increased system maturity at every opportunity. Enhancement of the self-organizing (Von Bertalanffy 1950) ability of the aquatic production system would seem to be within the grasp of current management technology. Atlan (1985) provided some necessary conditions for self-organization to occur in terms of redundancy (a kind of connectedness of system components) and resilience, that property which prevents the system from being completely destroyed by small perturbations. We have

discussed above our perception of how the Great Lakes guilds of fishes and the ecosystem development process confer resilience upon the Great Lakes fish communities. We assert that minimizing the external control requirements by managing in the direction of self-organization of the biological components is a minimum risk approach to sustain productivity of the system.

We referred earlier to agricultural production systems as examples of forced juvenescence. The immediate costs in energy and materials to sustain high productivity may (hopefully) be justified in that case, but the long-term price for increased *dependency* on nonrenewable sources of energy is not yet estimable. Managing fish communities is qualitatively different because the fish of interest to man operate at the tertiary and quaternary production levels as opposed to the primary and secondary levels. This elevates the costs of fish production based on artificial propagation and introduces a large degree of uncertainty in the management of natural systems. Intensive hatchery culture circumvents the primary and secondary production levels by direct protein subsidy. Pitcher and Hart (1982) pointed out that in the United Kingdom, 1 kg of rainbow trout (*Salmo gairdneri*) costs the energy equivalent of an equal weight of petroleum (largely) spent in taking the marine fishery by-catch for the production of the food.

The "reclamation" of small natural lakes by use of biocides followed by restocking with game fish was an approach to inland fishery management which was especially popular through the 1950's and 1960's (Northcote 1970). It was an enjuvenation procedure which worked best with the fish converting at the tertiary level (e.g. brook trout (*Salvelinus fontinalis*)) and in cases where access to other fish species was sufficiently limited to inhibit community maturation. In practice, retreatments were frequently required, and often the value of the harvested hatchery fish did not match the costs of the intensive control. In larger lakes, moreover, such precise channeling of energy-matter usually proved impractical.

The last notwithstanding, we hesitate to judge any effort to structure and maintain any form of fish community. It largely devolves to a question of how much cost society will commit to controlling specialized communities. Significant questions remain regarding the attainability and desirability of stability as a system property, and estimation of the costs of control.

In Fig. 4, we list eight options for open-water species mixes in the Great Lakes, in what we perceive to be a descending order of control costs. These costs cannot be quantified at this time, but our suspicion is that the increases from the bottom of the construct to the top rise exponentially.

Control costs can never go to zero as long as man is interested in fish and/or potable water from the lakes. Thus in the most natural kind of fish community there would always be costs associated with regulation of the fisheries and with maintenance and improvement of fish habitat. The requirement for sea lamprey control might ultimately be eliminated in a healthy system, but we believe that society will support lamprey control for the near future in order to maintain at least the fishery benefits currently being realized from the Great Lakes.

At the most artificial end of the control scale in Fig. 4, concerns for the genetic perpetuation of the highly successful stocks of chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmons will be matched by concerns for the conservation of their exotic prey fishes. In addition to the regulatory and sea lamprey control needs, one anticipates intensive directed fishing (and hunting) programs to control competitors and predators of these fish. This would clearly be a perpetual process, and in order to maintain the "fine-tuning" appropriate to control in the large systems, demands for real-time assessment will require major investments.

A point of concern in connection with Fig. 4 is that it treats the open-water systems as though they were independent of the other components of the fish communities. Lake Erie and each of the oligotrophic members of the chain support important walleye and other fisheries characteristic of the shallower waters. There have been successful programs to reintroduce walleye in some of the large bays, but in the main, walleye and the communities they integrate and depend on are self-sustaining where exploitation is controlled and water quality is adequate. One of the important lessons which emerged from application of Ryder's (1965) morphoedaphic index was that fish yields are only predictable on an integrated, whole-lake basis. This requires that the vectoring of materials and energy in the systems is naturally coherent and that the nearshore and offshore components of the fish communities are interdependent. Hurley and Christie (1977) discussed the recent role of migrant alewife and their progeny in the biological economy in the Bay of Quinte of Lake Ontario and speculated on an earlier, comparable role for whitefish and lake herring (*Coregonus artedii*). This use of common food resources by nearshore and offshore piscivores probably imposes upper limits on yields of the offshore salmonids (and thus on control costs) by way of the constraints imposed by the natural part of the system.

It has not been customary to aggregate control costs in the manner suggested by Fig. 4, but it clearly represents a useful approach for fishery development and management strategies. This was anticipated by Vallentyne (1973) who defined "demophoric" growth as the totality of human impact on the systems. Control costs will escalate in proportion to demophoric growth irrespective of the type of fish community designated for management. Understanding of control costs in this context requires that real benefits be measured in terms of relative performance of various fisheries as well as total benefits and that costs be computed across the gamut of management activities. Data for such analyses are collected, but not routinely addressed in this way, and in view of the present importance of defining the future mixes of fisheries and target species for the Great Lakes, it is clearly an urgent area for investigation. It is also important to note that "willingness to pay" is an economic attribute of the current generation of *users* and thus insufficient for estimation of the value of perpetuation of a renewable common property resource.

The concept of managing for system maturity has important implications for fishing strategies aimed at low control costs. For example, relaxing quotas in the face of an oncoming abundant year class is not necessarily the appropriate management response. It may be more suitable to maintain or tighten controls on the fishery until the year class accumulates enough biomass to regulate the production of the system. Devices such as "slot limits" (Colby 1984; Colby et al. 1987), the "proportional stock density index" (Anderson and Gutreuter 1983), and live release programs, although developed to meet other objectives, probably offer the best current opportunities for sustained yield management of attractive predator fisheries.

An equally clear inference from our analysis is that the rate of rehabilitation of natural fish communities in the Great Lakes is very sensitive to the longevity of the lake trout. Even very light

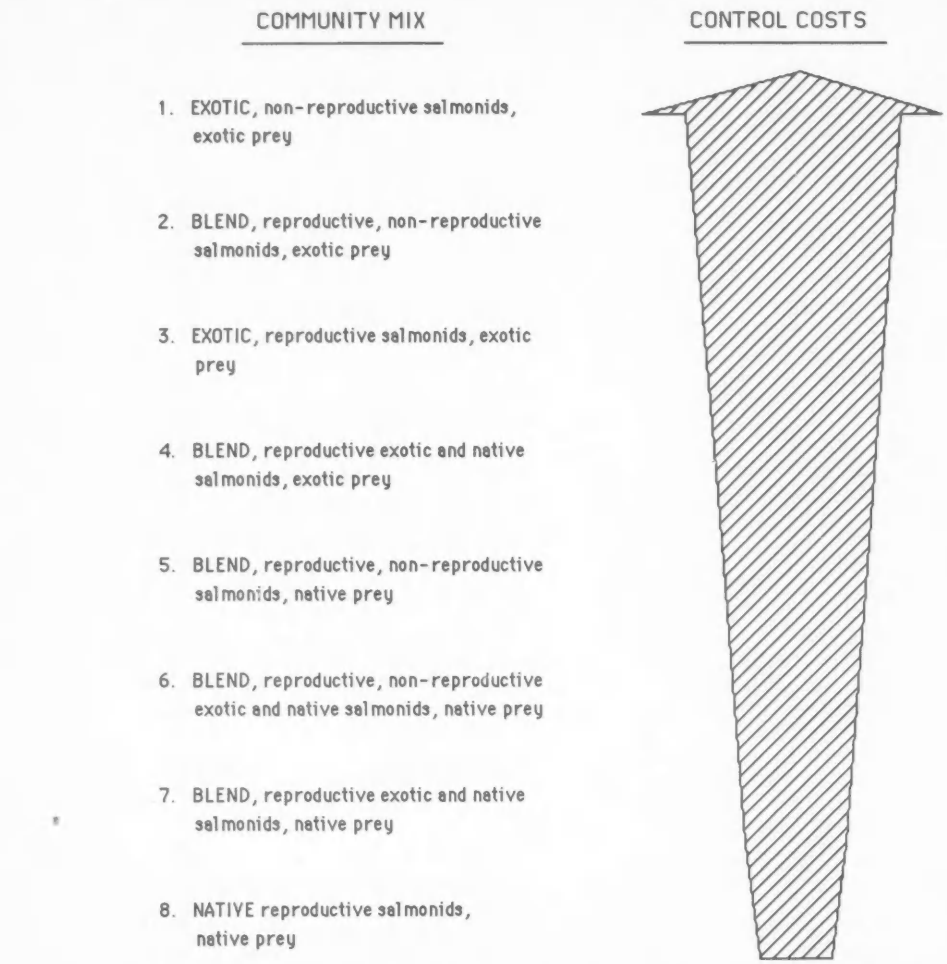

FIG. 4. Possible species assemblages for Great Lakes open-water fish communities in relation to costs required to maintain them.

exploitation may be sufficient to stall the reestablishment of natural propagation.

The periodic nature of the natural enjuvenation events contrasts with the more or less continuous application of cultural stresses and suggests that we can best mimic nature by pulsing the stresses so as to allow time for "system self-organization" between pulses. For fisheries where continuous allowable yields are unattractively low, there may be long-term advantages to cropping a target species heavily at intervals. The model depicted by Fig. 1 and 3 portrays an aquatic system with a biomass line across its span of logarithmic weight intervals which is level, on average, but disturbed by waves which move back and forth under the influence of external perturbations. The prediction of the model is that continuously overfishing piscivores in a simple algae–zooplankton–planktivore–piscivore system would have the effect of creating a standing wave such as illustrated in Fig. 5. This in turn suggests a systematic explanation for the apparently discordant findings that P/B is higher in smaller than in larger organisms, while yield predictions based on the morphoedaphic index (Ryder 1965) are independent of food chain length (Leach et al. 1987). Christie (1974) and Ryder et al. (1974) explained the phenomenon in terms of diversion of production into organisms either unmarketable or catchable only at excessive energy costs. Figure 5 suggests that where planktivore abundance is increased as a result of reduced piscivory, the resultant reduction in zooplankton creates excessive algae concentrations. These high densities do not result in reciprocal improvements in zooplankton density because of the short algal life spans (Patten's (1985) "storage" effect), and the surplus production goes to waste at the primary level. The market and energy considerations mentioned above still apply, but we argue that efforts to free the "bottleneck" by fishing down the planktivore biomass likely do not often succeed because of the numerous small planktivorous species and planktivorous young of many species. The reduction of the larger planktivores may in fact enhance planktivory by very young fish by the reduction of tertiary piscivory (Keast 1983). This construct satisfactorily fits the observations of Edgington (1984) on southern Lake Michigan and of Spencer and King (1984) on pond communities. Just how far the

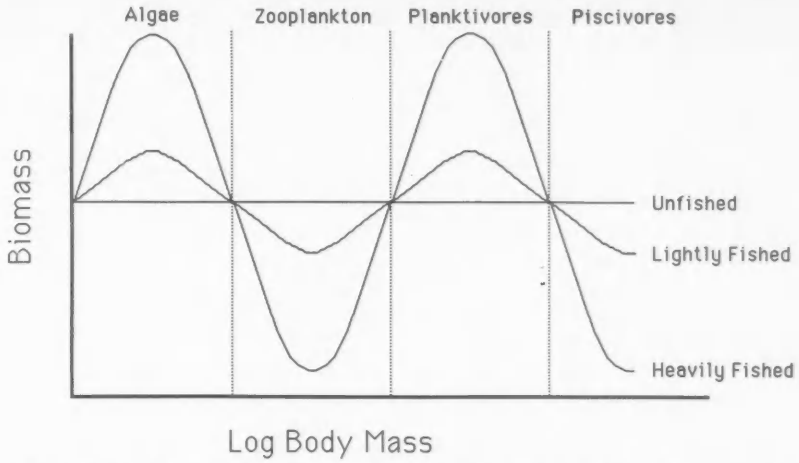

FIG. 5. Illustration of the standing wave effect in biomass fluctuation in simple ecosystems as a consequence of exploitation stress.

generality can be extended is unknown at present. The problem is an important one, however, and we suggest that this model provides a useful focus for further research in the area of particle size theory. Tests of the validity of the four-tiered model require substantially improved estimates of relative biomass and consumption than are now available and studies of systemic roles of benthivorous fishes and predacious zooplankton, in particular.

The biotic inertia principle has been discussed in relation to $r-K$ theory and to asymmetrical effects of "top-down" perturbation on the systems. These phenomena illustrate the perception of Patten and Odum (1981), Margalef (1985), and Patten (1985) that the role of an organism in the ecosystem increases in proportion to its age and size. From the contemporary management perspective it can be inferred that either overstocking or very modest overexploitation could lead to major destabilization of the aquatic community and concomitant yield uncertainties.

The enjuvenation principles discussed here apply equally well to fish habitat management. The medium cycle length changes associated with cattail (*Typha* sp.) marsh maturation and emergence have been identified and reversions are routinely used in waterfowl management, but there are few such practices in fisheries. In fact, protection against shoreline erosion either involves cement works to prevent enjuvenation or groins which reduce the enjuvenation effect and create macrophyte beds. This is probably the reason for the "Verbauung" effect, i.e. the restructuring of inshore areas, as a factor in the decline of European inland lake fisheries (Grimaldi 1972; Grimaldi and Numann 1972; Regier and Loftus 1972a, 1972b). This restructuring and hydroelectric power production may be examples of the ways in which shoreworks reduce the fish productivity of aquatic ecosystems, and they illustrate the profound way in which the ideas about natural enjuvenation cycles should affect our management approaches.

The analysis of Steedman and Regier (1987) identifies centers of organization for fish communities which are characteristically found in areas where cultural impacts like those above are prevalent. In terms of our model, all such effects act to create the standing wave of Fig. 5. Thus, the production potential represented by increased algal densities in eutrophied areas is largely wasted because the coincident turbidity and lowered dissolved oxygen concentrations differentially affect the piscivores. The effect is more direct in cases of losses of spawning habitat. We share the optimism of Steedman and Regier that very substantial remediation will be possible when the importance of the centers of organization to the coherent vectoring of energy-matter in the entire system is understood. Remediation and rehabilitation of these key areas represent part of the control costs associated with Fig. 4, and inevitably these costs will be higher in close proximity to human populations where habitat degradation has proceeded further. In the context of fish community structure, management for a healthy, internally regulated community can make the job of protecting the potable water supplies much less expensive, for example, by lower costs in municipal phosphate controls and filtration. Quantifying these relationships merits high research priority.

A useful distinction between mitigation and rehabilitation is that the former seeks to lessen immediate impact of human activity through definition of a "socially acceptable" altered state whereas the latter seeks to encourage self-organization of the aquatic ecosystem, thus internalizing control and *reducing the requirement for additional external control*.

From a long-term management perspective, man has no option but to attempt to gain perpetual manipulative control over the Great Lakes aquatic production systems. Points of departure between current management philosophies are merely divergent views on the degree of external control that will be required to maintain useful production from the lakes. One extreme is that degradation has progressed too far for any significant natural recovery whereas the view expressed here holds that the enjuvenation–maturation process is a general blueprint explicit only with respect to the *kinds* of stresses which might be removed or relaxed. This is a common dichotomy, perhaps best exemplified by the 1976 Reykjavic Symposium on the Breakdown and Recovery of Damaged Ecosystems (Holdgate and Woodman 1978). Recognizing this, Magnuson et al. (1980) offered a more specific blueprint for rehabilitation which deals with the average: "Restoration of many of the early qualities of the Great Lakes is a desirable goal, yet we will often have to settle for a partial restoration or rehabilitation." The point is

unquestionably valid, if for no other reason than that even with full restoration of the fisheries, Lake Superior, for example, will always be different because its fauna now includes smelt and sea lamprey. Assuming that Great Lakes degradation has progressed too far for recovery denies evidence to the contrary, presented at ASPY and SCOL, and generates a self-fulfilling prophecy that extensive continuing human intervention will ensure. We hope that the ASPY results are sufficient to reinforce this word of caution and to encourage development of understanding of natural recovery processes.

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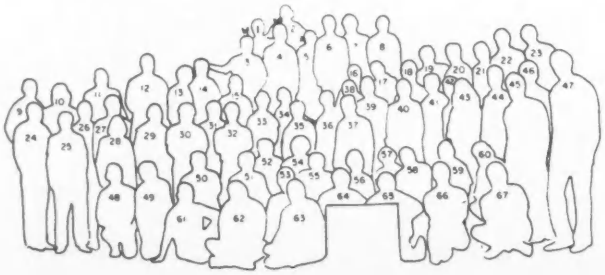

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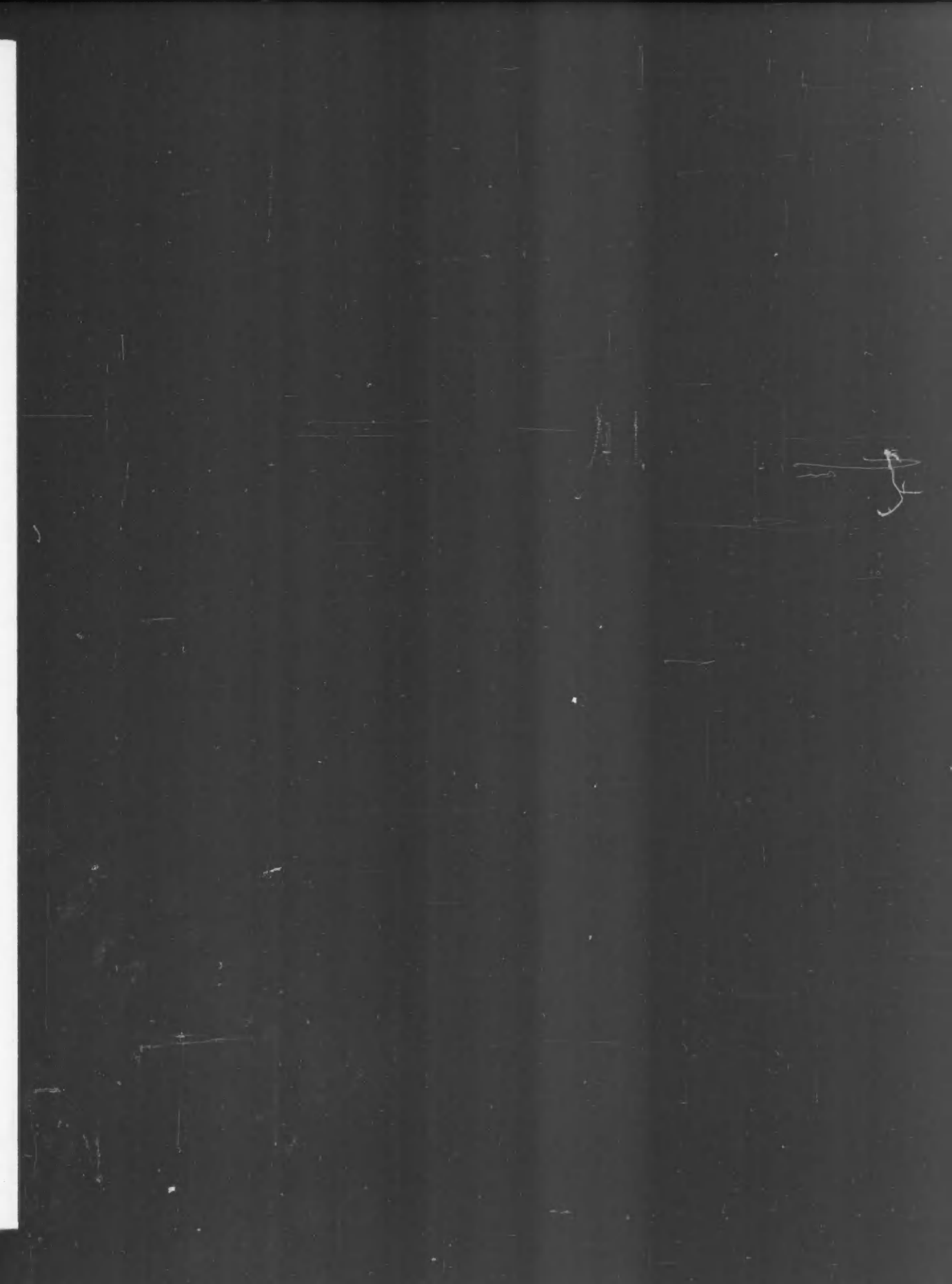
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